















# SMITHSONIAN

## MISCELLANEOUS COLLECTIONS

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VOL. 103

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"EVERY MAN IS A VALUABLE MEMBER OF SOCIETY WHO, BY HIS OBSERVATIONS, RESEARCHES,  
AND EXPERIMENTS, PROCURES KNOWLEDGE FOR MEN"—SMITHSON

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C. G. ABBOT,

*Secretary of the Smithsonian Institution.*





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VOLUME 103, NUMBER 1

DISTRIBUTION AND VARIATION OF THE  
HAWAIIAN TREE SNAIL *ACHATINELLA*  
*APEXFULVA* DIXON IN THE  
KOOLAU RANGE, OAHU

(WITH 12 PLATES)

BY

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BY D'ALTÉ A. WELCH

(WITH 12 PLATES)

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## INTRODUCTION

### SCOPE OF WORK

In a previous paper (Welch, 1938) the species *Achatinella mustelina* is studied. The present paper continues the work on Hawaiian tree snails and deals with the species *Achatinella apexfulva*, also of the island of Oahu. Does the same variation or series of variations occur

in *A. apexfulva* of the Koolau Range as in *A. mustelina* of the Waianae Mountains?

During the 7 years I spent in Hawaii studying *Achatinella* I was greatly helped in acquiring a background for the present work by Dr. C. M. Cooke, Jr. Working under Dr. Cooke, I also learned many methods of studying and preparing material which greatly facilitated my work. I am also indebted to Dr. E. A. Andrews, Dr. Henry A. Pilsbry, Dr. H. B. Baker, and Dr. Ernst Mayr for criticisms and advice in the preparation of the manuscript. Dr. F. Raymond Fosberg was most helpful in identifying all genera of Hawaiian plant names given by various collectors of shells. I also wish to express appreciation to the following for various courtesies and favors: Dr. Paul Bartsch, W. J. Clench, W. T. Calman, Col. A. J. Peile, J. R. le B. Tomlin, G. S. Robson, Dr. Paul Galstoff, Dr. Gilbert D. Harris, Dr. C. E. McClung, Dr. Peter H. Buck, Dr. Herbert Gregory, the Trustees of the Bernice P. Bishop Museum, and the authorities of the United States National Museum.

The ground work of this paper was done at the Bernice P. Bishop Museum in Honolulu, the writing of the paper was carried on at the United States Bureau of Fisheries at Woods Hole, the Zoological Laboratory of the University of Pennsylvania, the Zoological Department of the Johns Hopkins University, and the Zoological Department of Barat College, Lake Forest, Ill. I wish to thank these institutions for granting me facilities for work.

#### PLACE NAMES OF THE KOOLAU RANGE

Most of the names of the valleys or gulches of the Koolau Range are well known, but the names of some have never appeared on a Government map. Other gulch names have not been known, and still other gulches, although their names are well known, contain large subgulches that need to be designated by some name in order that localities may be described exactly.

Pilsbry and Cooke (1912-1914, p. 277) published a rough diagrammatic sketch map of the northwestern half of the Koolau Range in which they included the new names Kalaikoa, Ahonui, Main Poamoho, Central Poamoho, West Poamoho, Kawaihalona, and Luapo. This map was compiled from field notes made by Irwin Spalding and is the first published map showing the approximate regions occupied by colonies of *Achatinella*. Many of these names do not exist on the advance sheets of the United States Geological Survey topographic sheets of Oahu, Hawaiian Islands, 1/20,000, which form the standard map I used for plotting all localities of

*Achatinella* and from which all maps published in this paper have been compiled. Therefore a considerable amount of work has been done to check the place names on the Pilsbry-Cooke map and to ascertain the place names of all valleys not yet published.

I am indebted to the following people for help in this work: The Bishop Estate for access to maps, Miss Jane L. Winne for place

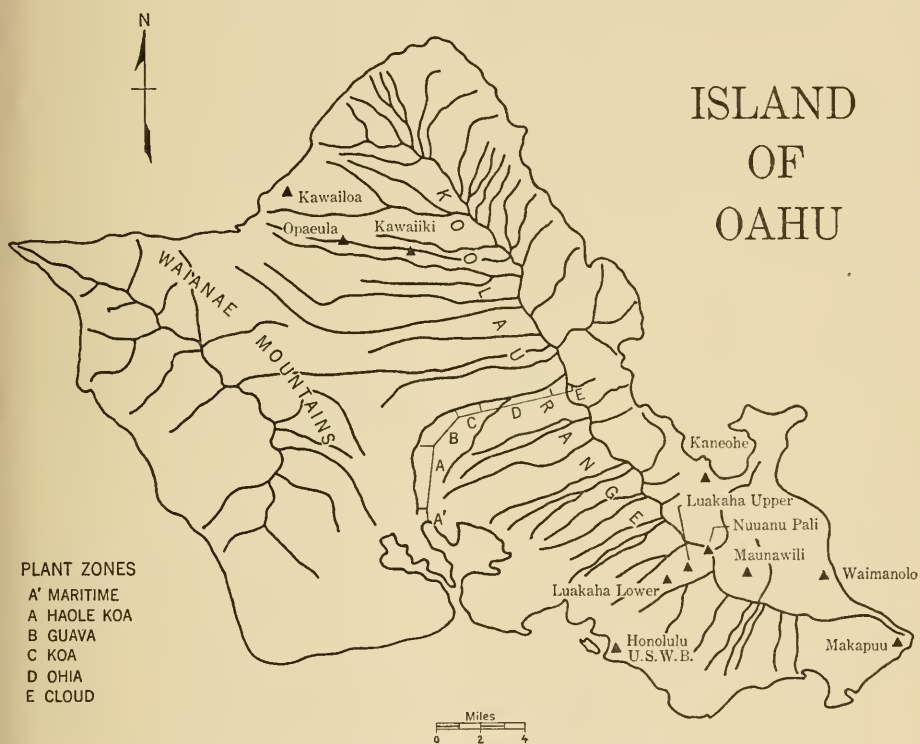


FIG. 1.—Island of Oahu, showing the plant zones in Kipapa Gulch (after Hosaka) and the location of rain-gage stations in the Koolau Range. Ridges outlined in solid lines.

names obtained from an old Hawaiian native to the district of Maunaloa; Manuel Baptista, a former cattle ranger native to the districts of Kalauao and Waiawa; G. D. Robinson; William Holt, a former cattle ranger in the regions of Wahiawa and Paala; Benny Pulaa, a Hawaiian native to the districts of Kawaiiloa, Waimea, and the northern section of Oahu.

The Koolau Range is divided into six large land grants or districts which are numbered A to F on figure 2, p. 4. Within these large

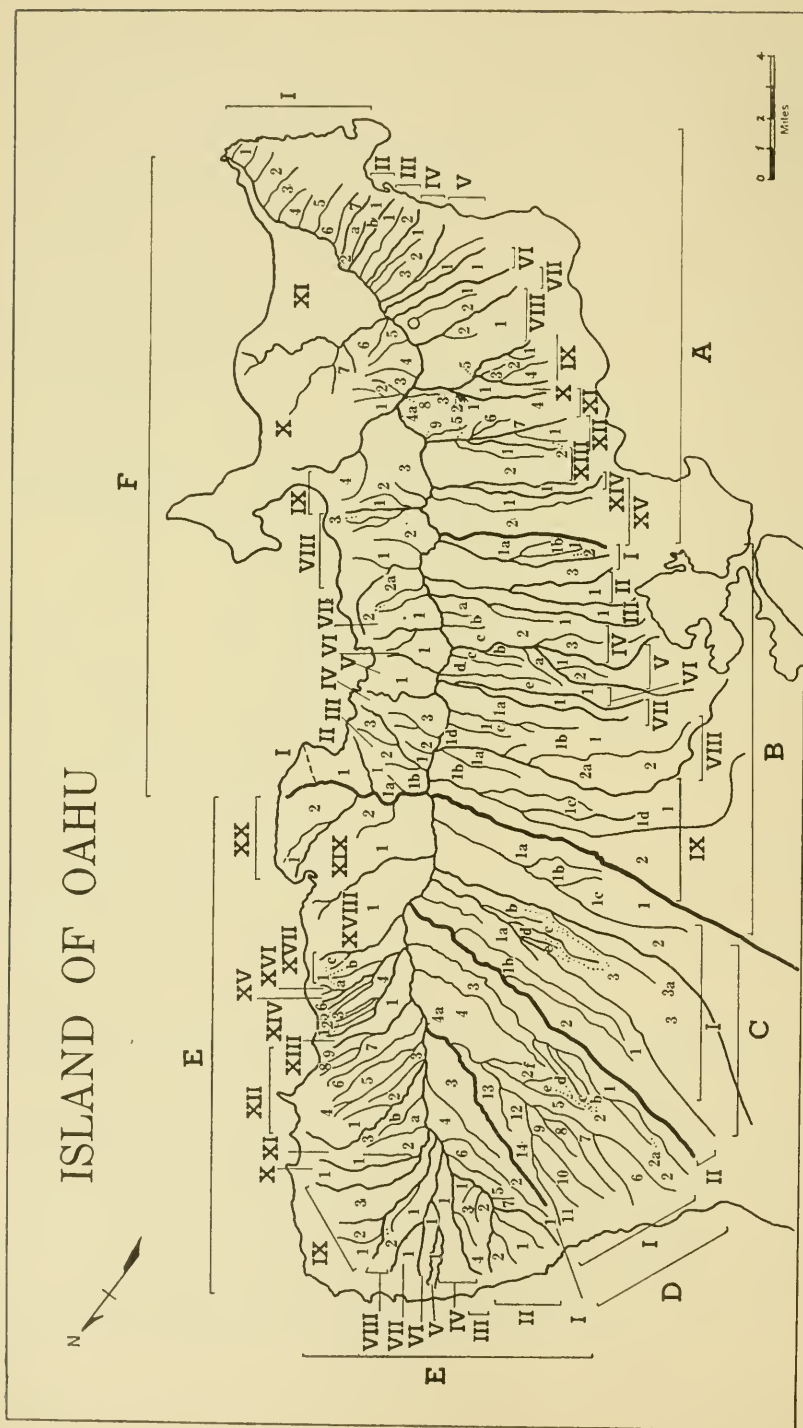


FIG. 2.—Key map to the place names of the Koolau Range. Ridges outlined in black.

districts are smaller districts or subdistricts indicated by Roman numerals, which may include a single valley or gulch with the same name or several valleys with different names. The valleys or gulches within a subdistrict are numbered in Arabic. In the discussion of place names, all names not published on the United States Geological Survey topographic advance sheets of the island of Oahu will have in parentheses the names of the authorities after them. Main valleys or gulches are often subdivided by the author for convenience into north, south, east, west, or central. These main valley subdivisions may be broken up again into north or south branches.

Figures 1 and 3-6 were drawn by Gordon Brett Littlepage from maps compiled by me. Figures 2, 7, 8 were drawn by me. All maps are compiled from the United States Geological Survey topographic advance sheets of the island of Oahu. Ridges on all maps are represented by lines.

*Place names of the Koolau Range*

A. Honolulu District.

I. Maunalua.

- 1, Kealakipapa Valley; 2, Mauuwaii Valley; 3, Kalama Valley; 4, Kamiloiki Valley; 5, Kamilonui Valley; 6, Hahaione Valley; 7, Kaalakei Valley (Bishop Estate maps: J. Winne).

II. Kuliouou.

- 1, Kuliouou Gulch; 1a, East Branch (Welch); 1b, West Branch (Welch); 2, Puu O Kona.

III. Niu.

- 1, East Niu Gulch; 2, West Niu Gulch. (1-2 Welch.)

IV. Wailupe.

- 1, Kului Gulch; 2, Lauaupoe Gulch; 3, Wailupe Gulch.

V. Waialae Iki.

- 1, Kapakahi Gulch (in this paper Waialae Iki Gulch will be used in preference to Kapakahi Gulch).

VI. Waialae Nui.

- 1, Waialae Nui Gulch (spelled Waialaenui on U. S. Geol. Surv. topogr. advance sheets).

VII. Palolo.

- 1, Waiomao Stream; 2, Pukele Stream.

VIII. Manoa.

- 1, Manoa Stream; 2, East Manoa Stream (Welch).

IX. Makiki. (This name is not on the U. S. Geol. Surv. topogr. advance sheets, but it is a well-known name and has been in use by shell collectors for many years.)

- 1, Maunalaha Stream; 2, Moleka Stream; 3, Kanealole Stream; 4, Kanaha Stream; 5, Puu Ohia (Tantalus).

X. Pauoa.

- 1, Pauoa Valley.

## XI. Nuuanu.

- 1, Glen Ada; 2, Glen Elm; 3, Lulumahu Valley; 4, Nuuanu Stream; 4a, Nuuanu Pali; 5, Hillerbrand's Glen; 6, Maole Stream; 7, Waio-lani Stream (Rook's Valley, Cooke); 8, Puu Konahuanui; 9, Puu Lanihuli. (1-3, 5, place names given by Dr. Cooke to certain unnamed places where shells were collected.)

## XII. Kapalama.

- 1, Niuhelewai Stream; 2, Kapalama Stream.

## XIII. Kalihi.

- 1, Kamanaiki Stream; 2, Kalihi Stream.

## XIV. Kahauiki.

- 1, Kahauiki Stream.

## XV. Moanalua.

- 1, Manaiki Stream; 2, Moanalua Stream.

## B. Ewa District.

## I. Halawa.

- 1, South Halawa Stream; 1a, South Branch (Welch); 1b, North Branch (Welch); 2, Central Halawa Stream (Welch); 3, North Halawa Stream.

## II. Aiea.

- 1, Aiea Stream.

## III. Kalauao.

- 1, Kalauao Stream.

## IV. Waimalu.

- 1, Hanaiki Stream (Bishop Estate maps); 2, Waimalu Stream; 2a, South Branch; 2b, Central Branch; 2c, North Branch; 3, Punanani Gulch. (2a-2c Welch.)

## V. Waiau.

- 1, South Waiau Gulch; 2, North Waiau Gulch. (1-2 Welch.)

## VI. Waimano.

- 1, Waimano Stream; 1a, South Waimano Stream; 1b, South Central Waimano Stream; 1c, Central Waimano Stream; 1d, North Central Waimano Stream; 1e, North Waimano Stream. (1a-1e Welch.) 1a-1c are in the district of Waiau but for convenience have been considered part of the Waimano Stream system.

## VII. Manana.

- 1, Manana Stream.

## VIII. Waiawa.

- 1, Waiawa Stream; 1a, South Waiawa Stream (Welch); 1b, North Waiawa Stream (Welch); 1c, North Waiawa Stream, South Branch (Welch); 1d, North Waiawa Stream, North Branch (Welch); 2, Panakauahi Gulch; 2a, Panihakea Gulch (Baptista), the upper part of Panakauahi Gulch. (Mr. Baptista tells me that the Hawaiian name for South Waiawa Stream is Keahupuolo Stream. However the shells in the collection are labeled South Waiawa and I think it is advisable to use this name in preference to Keahupuolo.)



## IX. Waipio.

- 1, Kipapa Gulch; 1a, South Kipapa Gulch; 1b, Central Kipapa Gulch; 1c, North Kipapa Gulch, second North Branch; 1d, North Kipapa Gulch, first North Branch. (G. D. Robinson tells me that only the lower portion of the valley should be called Kipapa Gulch. The upper portion is Waipio Valley. Kipapa was the crossing place in the gulch where stones were placed together to form a road. A. F. Judd also considers Waipio to be the correct name of the Gulch. However, since the collections and the U. S. Geol. Surv. topogr. advance sheets use the name Kipapa, I believe it would be confusing to use Waipio.); 2, Waikakalaua Stream. (1a-1d Welch.)

## C. Wahiawa District.

## I. Waianae Uka.

- 1, South Kaukonahua Stream; 1a, South Kaukonahua, South Branch (Welch) (this may be Gulick's Kalaikoa District, or Kalaikoa may have included all of South Kaukonahua Stream); 1b, South Kaukonahua, Central Branch (Welch); 1c, South Kaukonahua, North Branch (Welch); 2, North Kaukonahua Stream. (Mr. Robinson showed me a place where formerly stood a boulder called Oahunui. The saying was that if anybody walked around this rock in a spiral starting at the bottom and going up to the top he would have gone around the island of Oahu. Ahonui may be a corruption of the word Oahunui. The place shown me is in the South Kaukonahua at an elevation of about 900 feet, below or opposite the North Branch of the South Kaukonahua. Pilsbry and Cooke, on the authority of Spalding, who in turn probably obtained accurate information from J. S. Emerson, an authority on Hawaiian place names, places Kalaikoa and Ahonui of Gulick between the North and South Kaukinehua (a misspelling for Kaukonahua), Kalaikoa being in the Central Branch, and Ahonui in the North Branch, of the South Kaukonahua. This ties in with Mr. Robinson's information. Ahonui of Gulick, however, may have included this region as well as North Kaukonahua Gulch. The Gulick shells represent a mixture from over a considerable area.); 3, Poamoho Stream; 3a, South Poamoho Stream; 3b, Central Poamoho Stream (Main Poamoho, Pilsbry and Cooke); 3c, Central Poamoho Stream, North Branch; 3d, North Poamoho Stream (Central Poamoho?, Pilsbry and Cooke); 3e, North Poamoho Stream, North Branch (West Poamoho, Pilsbry and Cooke). (3a-3e Welch.)

## II. Paala Uka.

- 1, Heleman Stream; 1a, South Heleman Stream (Welch); 1b, North Heleman Stream (Welch); 2, Kawaihalona Gulch (Holt, Robinson, Pulaa, Pilsbry and Cooke).

## D. Waialua District.

## I. Kawailoa.

- 1, Opaaula Gulch; 2, Kawailoa Gulch; 2a, First South Branch; 2b, Second South Branch; 2c, Third South Branch; 2d, Fourth South Branch; 2e, First North Branch; 2f, Second North Branch (2a-2f Welch); 3, Kawaiiki Gulch; 4, Kawainui Gulch; 4a, Puu Kainapua; 5, Kawaiipapa Gulch (Pulaa) (this Gulch will always be

referred to as Kawaipapa, Kawailoa Gulch, because this place name occurs elsewhere in the Koolau Range); 6, Ukoa Gulch; 7, Kukaiohiki Gulch; 8, Keamanea Gulch; 9, Kaluapo Gulch (Luapo, Pilsbry and Cooke); 10, Kaalaea Gulch; 11, Kaluahole Gulch; 12, Waoala Gulch (wrongly spelled Waiola on the U. S. Geol. Surv. topogr. advance sheets); 13, Huluela Gulch; 14, Kawaikoele Stream. (5-13 Pulaa.)

E. Koolauloa District.

I. Waimea.

1, Waimea River; 2, Kamananui Stream; 3, Kolokini Stream (Pulaa); 4, Namahana Stream (Pulaa); 5, Elehaha Stream; 6, Kawaieli Stream (Pulaa). (Mr. Pulaa tells me that the Kawaieli Stream is where the Elehaha Stream is marked on the map. However, for convenience I shall not change the position of the Elehaha Stream on the U. S. Geol. Surv. map but shall consider the stream to the south the Kawaieli Stream instead of the Elehaha.) ; 7, Kauwalu Stream.

II. Pupukea.

1, Kalunawaikaala Stream; 2, Pakulena Stream.

III. Paumalu.

1, Paumalu Stream; 2, Kaleleiki Stream; 3, Kawaipi Stream; 4, Aimu Stream.

IV. Kaunala.

1, Kaunala Gulch.

V. Waialea.

1, Waialea Gulch.

VI. Pahipahialua.

1, Pahipahialua Gulch.

VII. Opana.

1, Kawela Gulch.

VIII. Hanakaoe.

1, Oio Stream; 2, East Oio Stream.

IX. Kahuku.

1, Hoolapa Gulch; 2, Kalaeokahipa Gulch; 3, Ohia ai Gulch.

X. Keana.

1, Keaaulu Gulch.

XI. Malaekahana.

1, Lamaloa Gulch; 2, Hiina Gulch; 3, Malaekahana Stream; 3a, North Malaekahana Stream; 3b, South Malaekahana Stream. (3a-3b Welch.)

XII. Laie.

1, Omao Gulch; 2, Kaluakauila Gulch; 3, Kahawainui Gulch; 4, Kaaooa Gulch; 5, Ihiili Gulch; 6, Wailce Gulch; 7, Koloa Gulch; 8, Aakaki Gulch; 9, Kokolofio Gulch.

XIII. Kaipapau.

1, Kaipapau Gulch.

XIV. Hauula.

1, Waipilopilo Gulch; 2, Hanaimoa Gulch; 3, Kawaipapa Gulch; 4, Maakua Gulch; 5, Papali Gulch; 6, Punaiki Gulch.

XV. Makao.



## XVI. Kapaka.

## XVII. Kaluanui.

- 1, Kaluanui Stream; 1a, North Kaluanui Stream; 1b, Central Kaluanui Stream; 1c, South Kaluanui Stream. (1a-1c Welch.)

## XVIII. Punaluu.

- 1, Punaluu Stream.

## XIX. Kahana.

- 1, Kahana Stream; 2, Kawa Stream.

## XX. Kaaawa.

- 1, Olona Gulch (Meinecke), or Weliweli Gulch (Oswald). (I am using the name Olona because I have heard from some source other than Meinecke that that was the correct name, and I have heard of Weliweli from only one source. However, I am not at all sure which is correct.); 2, Kaaawa Stream.

## F. Koolaupoko District.

## I. Kualoa.

## II. Hakipuu.

- 1, Hakipuu Stream.

## III. Waikane.

- 1, Waikane Stream; 1a, North Branch; 1b, South Branch; 2, Waikēkee Stream; 3, South Waikane Stream (Welch).

## IV. Waiahole.

- 1, Uwau Stream; 2, Waianu Stream; 3, Waiahole Stream.

## V. Kaalaea.

- 1, Kaalaea Stream.

## VI. Waihee.

- 1, Waihee Stream.

## VII. Kahaluu.

- 1, Kahaluu Stream; 2, Ahuimanu Stream; 2a, East Ahuimanu Stream (Welch).

## VIII. Heeia.

- 1, Iolikaa Valley; 2, Haiku Valley; 3, Keaahala Stream.

## IX. Kaneohe.

- 1, Kaneohe Stream; 2, Luluku Stream; 3, Kamooalii Stream; 4, Kawa Stream.

## X. Kailua.

- 1, Kahanaiki Stream; 2, Palapu Stream; 3, Omao Stream; 4, Maunawili Stream; 5, Aiuoni Stream; 6, Makawao Stream; 7, Olomana Stream.

## XI. Waimanolo.

## CLIMATOLOGICAL DATA AND PHYSIOGRAPHY

The main division ridge or backbone ridge of the Koolau Range extends for 37 miles along a northwest and a southeast axis in the eastern portion of the island of Oahu. Parallel to it are the Waianae Mountains, which are of smaller extent and lie in the western part of the island. The windward slope of the Koolau Range is made up of high cliffs and short ridges usually less than 3 or 4 miles long.

The leeward slope for the most part has long fingerlike ridges which may be as much as 15 miles in length and is much drier than the windward slope. The trade winds blow from the northeast and hit the high wall of cliffs on the windward slope. The maximum rainfall resulting from the rising of the moisture-laden trade winds over the mountain wall falls not on the crest of the range but leeward of the summit. This is shown in table 1, where a series of precipitation records obtained from a station at Nuuanu Pali, at the summit of the Koolau Range, shows a lower rainfall than at Luakaha, below the summit of the range. At a still lower elevation the rainfall drops considerably at the Honolulu United States Weather Bureau station. Table 1 also shows a greater precipitation at stations on the windward

TABLE 1.—*Annual precipitation records in the Koolau Range*

Station	Elevation in feet	Precipitation in inches		
		1916	1917	1918
Kaneohe .....	100	58.92		97.37
Maunawili .....	250	93.58	85.53	122.17
Waimanolo .....	25	55.80	63.19	66.90
Nuuanu Pali .....	1,136	123.30	119.00	136.00
Luakaha (upper) .....	1,028	196.99	159.19	202.61
Luakaha (lower) .....	881	175.50	146.07	187.88
Honolulu (U. S. Weather Bur.).....	111	44.96	46.64	37.46
Makapuu .....	570	37.97	51.44	46.64
Kawaiiki .....	1,185	121.94	105.08	107.32
Opauala .....	1,100	80.46	74.55	81.83
Kawailoa .....	185		38.31	46.90

side of the island, such as Kaneohe and Waimanolo, than at the Honolulu station on the leeward side. Table 1 was compiled from "Climatological Data," published by the United States Department of Agriculture.

Hosaka (1937) gives some interesting data on temperature, relative humidity, soil moisture, and soil temperature in Kipapa Gulch, which is in about the center of the Koolau Range. The general trend is a decrease in temperature and an increase in humidity with increase in elevation. The average annual rainfall taken over a period of 5 to 36 years in Kipapa Gulch is as follows: At 59.05 to 196.85 feet (Haole Koa zone), 23.07 to 24.33 inches; at 377.28 feet (Haole Koa zone) to 672.54 feet (Guava zone), 47.77 to 47.49 inches; at 738.16 feet (Koa zone), 79.05 inches; at 1,797.82 feet (Ohia zone), 199.01 inches. The atmospheric temperature records from March 19 to November 26, 1933, show an average temperature at 246.06 feet

(Haole Koa zone) of 84.56° Fahrenheit; at 738.16 feet (Guava zone), 77°; at 1,000.61 feet (Koa zone), 75°2; at 1,591.2 feet (Ohia zone), 71°6; at 2,198.2 feet (Cloud zone), 70°7 (see below for explanation of plant zones, and fig. 1, p. 3).

The extreme southeastern section of the Koolau Range is exceedingly dry (see table 1, Makapuu). The main division ridge rises toward the west to 2,200 feet above Kuliouou Gulch, at Puu O Kona (fig. 7, p. 194). Between Puu O Kona and Konahuanui the backbone ridge fluctuates in height from 2,200 to 2,600 feet. At the head of Nuuanu Valley the division ridge rises to 3,105 feet at the high peak of Konahuanui, descends at Nuuanu Pali to 1,186 feet, and rises again to 2,700 feet at Puu Lanihuli. To the northeast of Puu Lanihuli the backbone ridge fluctuates in height from 2,250 to 2,800 feet. The usual elevation would be roughly 2,400 to 2,500 feet. Above Kawainui Gulch in Kawailoa the backbone ridge begins to drop in elevation near Puu Kainapuaa. From Puu Kainapuaa to the head of Ohia ai Gulch there is a gradual descent from 2,250 to 1,750 feet. From Ohia ai Gulch to the head of Pupukea the drop is a gradual one from 1,750 to 900 feet.

*Achatinella apexfulva* today occurs almost exclusively on the leeward slope of the Koolau Range. The material in this paper comes from 45 ridges and 11 valleys. Five of the ridges are on the windward slope of the Koolau Range. The upper limit at which *A. apexfulva* occurs is usually from  $\frac{1}{2}$  mile to  $1\frac{1}{2}$  miles from the backbone ridge, but it may be farther on some ridges which have not been collected at higher elevations. The lower edge of the collectable area varies northwest of Nuuanu Valley to Kawailoa (fig. 7) from  $2\frac{1}{2}$  to  $5\frac{3}{4}$  miles in a straight line from the backbone ridge. In Nuuanu Valley and on the Niu-Wailupe Ridge the localities are less than a quarter of a mile from the summit of the backbone ridge. These two regions are exceptions to the general rule. It is strange that this species is not found on the backbone ridge as are other species. But as far as the material from carefully plotted localities is concerned no specimens are from the backbone ridge.

Hosaka (1937, pp. 179-180), in discussing the ecology of Kipapa Gulch distinguishes six plant zones, which are copied on figure 1. They are as follows: Maritime zone, Haole Koa zone, Guava zone, Koa zone, Ohia zone, and the Cloud zone. Hosaka writes:

In the Guava Zone *Psidium Guayava* and *Lantana Camara* are most common. Above this region is the Koa Zone, dominated by *Acacia Koa* and *Gleichenia linearis* on the slopes, and by *Aleurites moluccana* in the gully bottoms. The central portion of the native forest, the Ohia Zone, is dominated by *Metrosideros*

*collina* (*Ohia lehua*), a tree towering 15 meters or more above the ground. The cloud zone is characterized by low, dwarfed shrubs in more sheltered parts and by mat-forming *Panicum*, *Paspalum*, *Isachne*, and mosses in exposed windswept areas.

The maritime, Haole Koa, and Guava zones are mostly made up of introduced plants, according to Hosaka; the Ohia and Cloud zones contain the largest number of endemic species. The Ohia zone has the largest number of indigenous plants.

*Achatinella apcxfulva* is almost entirely confined to the Ohia zone and the upper portion of the Koa zone. The width of the Ohia zone obviously varies in different parts of the range. In the Nuuanu Valley region the Ohia zone is comparatively narrow; to the west, near the Poamoho Stream, it is undoubtedly wider than at Kipapa Gulch.

#### MATERIAL AND METHODS

Over 11,302 shells were studied, the majority of which are from 287 localities. Out of this number 6,707 adult shells were measured from lots containing 5 or more shells and having a length range of at least 3 length classes. The total number of adults from plotted localities is 3,687, of which all but 283 were collected by W. Meinecke. Mr. Meinecke is the first person to make a large collection of *Achatinella* from the Koolau Range with the localities plotted on a good map such as the United States Geological Survey topographic advance sheets of the map of Oahu. All his localities prior to 1933 were plotted from memory; after that date, up to 1937, he again collected many of his former localities and many new ones, so that many errors made in plotting from memory are checked and corrected. Mr. Meinecke is such an unusually careful worker, with such an extraordinary ability to work with maps, that I have the greatest confidence in the exact plotting of his localities. This opinion is further strengthened by a check of some of his localities, all of which were found to be correctly plotted. A few of his localities collected before July 1932 are not dependable—in fact, this comment applies to all localities collected by anyone prior to 1932, with the exception of the localities of Dr. C. M. Cooke, Jr., in Nuuanu Valley which were mapped by sketch maps made in the field.

Other collectors who have supplied shells with locality data plotted on the United States Geological Survey topographic advance sheets and collected since 1932 are G. W. Russ, H. Lenke, and H. Lenke, Jr.

From localities that are not plotted on any map come 3,002 adult shells; they are mostly localized from the Meinecke and other care-

fully collected material. The exact locality of 350 of these, mostly extinct shells from the Gulick collection in the Bishop Museum, is unknown. The remainder of the shells were collected by W. D. Wilder, O. H. Emerson, J. S. Emerson, L. A. Thurston, C. M. Cooke, Jr., R. A. Cooke, C. H. Cooke, D. D. Baldwin, E. D. Baldwin, E. Lyman, A. F. Judd, and I. Spalding.

Type specimens of all previously described forms were studied whenever possible. Those in the British Museum were photographed by E. J. Manley, those in the Academy of Natural Sciences of Philadelphia by Miss Helen Winchester, those in the Museum of Comparative Zoology by the museum photographer, and those in the Bishop Museum by Kenneth Emory. The remaining shells and the holotypes of all new subspecies figured in this paper were photographed by E. Bafford, of Baltimore, and myself.

The type of *A. swiftii* Newcomb and *A. apexfulva* Dixon were among the few types not obtained for study. The type of *A. a. swiftii* should be in the British Museum but could not be located. Possibly if search were made again it would be found labeled *A. a. turgida*. The lot labeled *A. a. swiftii* is not the type lot.

The data concerning localities are of four types. All localities that were plotted from memory or prior to 1932 have an asterisk (\*) after the locality number. If the locality was collected after 1932, or if an old locality prior to 1932 has been again collected and proved correct, the locality number alone is given. A question mark (?) after the locality number indicates that there is some doubt in my mind as to the correct plotting of the material or that the material has been localized from another collector's material. All localities known only as to approximate regions and plotted years after collecting also have one question mark. Two question marks (??) after a locality or area indicate that the locality is believed to be somewhere in the approximate region, but there is no data to substantiate the plotting. The plotting of the locality may be based on the form and color pattern of the shell and what is known of shell variation in adjacent localities.

As a general rule the greatest dimension of a locality collected after 1932 is not over 100 or 200 yards, but some localities collected prior to, and even some after, this date reach an extent of a quarter of a mile or even as much as a mile. An attempt has been made to plot on the locality maps (figs. 3-6) the exact location and extent of each locality. Therefore the size of a locality and the distance between localities can be estimated from the scale of miles on each map.



Through necessity the circles denoting localities are drawn larger than the actual scale size of the localities in order that they may be seen.

All shells collected prior to 1932 were live shells. After 1932 the lots contained live and dead shells. The majority of shells measured were live specimens.

In the list of localities found with each subspecies, all lots containing less than five adult specimens have the number of dextral and sinistral specimens enumerated. If the number of adults in a lot is five or more, the number of dextrals and sinistrals, the length range, and the mean length of the shell are given in table 2, p. 15. All locality place names in the text are put in boldface type. In the Gulick lots only the type locality or localities which probably contained the subspecies are put in boldface type. Other localities which I consider doubtful are put in ordinary type.

When material is quoted under each form, the catalog numbers of the lot are quoted only when necessary. Most of the Meinecke, Russ, Cooke, and Lemke material has locality numbers, and is sufficiently distinct so as not to require the quotation of catalog numbers. All lots labeled Cooke, stand for Dr. C. M. Cooke. All lots not having locality numbers have catalog numbers given. The Gulick lots have no catalog numbers given because the Gulick lots have been selected from lots containing a mixture of color forms or subspecies and are not yet recataloged. However, the catalog numbers of the figured shells are given in the explanation of plates.

Methods of collecting material and recording localities on map tracings taken from the United States Geological Survey topographic advance sheets, the manner in which the shells are graded into length groups (table 2, p. 15), and the selecting of the typical or usual form of the shell are the same as those already described for *A. mustelina* (Welch, 1938). The only addition that should be made is the method of counting the number of whorls, which is the same as that described by Pilsbry (1939, p. xi). All holotypes of new subspecies have the usual form and color pattern of the shell unless otherwise stated.

All grading of shells into length groups for table 2, page 15, was done by two W. P. A. workers. Many of the lots were remeasured by me and found to be correct. Since the shells are all graded by the measuring rod described for *A. mustelina* (Welch, 1938, p. 12), I think there is little chance of error as far as has been ascertained from remeasuring lots here and there at random.

The following abbreviations are used in citations of museum shell lots, and in the references to the literature.

ANSP, Academy of Natural Sciences of Philadelphia

BM, British Museum

BBM, Bernice P. Bishop Museum

MCZ, Museum of Comparative Zoology

HL, Herman Lemke collection

Man. Conch., Manual of Conchology (second series)

The location of types is stated in the explanation of plates beginning on page 208.

TABLE 2.—Data on Material

Subspecies	Area	Collector†	Locality	Adults	Mean length	Length range	Dex- tral	Sinis- tral
REGION I.††								
Region of ridge complex 1, zones I and II.					mm.	mm.		
<i>A. a. forbesiana</i> .....	6??	Gulick	Waialae	11	17.0	16.5-18.5	10	10
<i>A. a. fuscostriata</i> .....	7??	Gulick	Palolo	39	16.5	15.5-18.5	3	46
<i>A. a. fuscostriata</i> .....	7??	Gulick	Waialae	14	17.0	15.5-18.5	..	26
<i>A. a. fuscostriata</i> .....	7??	Gulick	Wailupe	12	17.0	16.5-18.5	..	23
<i>A. a. simulator</i> .....	?	Gulick	Palolo	24	17.0	16.5-18.5	3	37
<i>A. a. buena</i> .....	?	All lots	....	11	17.0	16.5-18.5	..	21
Ridge complex 1, zones II and III.								
† <i>A. a. muricolor</i> .....	1	Meinecke, 1926	41-4*	101	17.5	15.5-19.5	..	170
† <i>A. a. muricolor</i> .....	1	Meinecke	41A-1*	11	18.5	16.5-19.5	..	12
† <i>A. a. muricolor</i> .....	1	Meinecke	41B-4*	4	18.0	16.5-19.5	..	6
† <i>A. a. waialaeensis</i> ....	2	Meinecke, 1933	51Aa	16	18.5	17.5-19.5	..	20
† <i>A. a. waialaeensis</i> ....	2	Meinecke	50A*	16	18.0	17.5-19.5	1	23
<i>A. a. waialaeensis</i> ....	2?	O. H. Emerson, 1916	....	16	19.5	18.5-20.5	..	23
† <i>A. a. simulator</i> var. 1..	4	Meinecke	62	15	18.0	16.5-19.5	21	..
Ridge complex 2, zone III.								
† <i>A. a. vittata</i> var. 1....	8	Meinecke	90A*	12	17.5	15.5-20.5	..	44
† <i>A. a. vittata</i> var. 1....	8	Meinecke, 1923	91A*	37	18.0	16.5-19.5	..	72
† <i>A. a. vittata</i> var. 1....	8	Meinecke, 1925	91A*	57	18.0	16.5-19.5	..	91
† <i>A. a. vittata</i> var. 1....	8	Meinecke, 1926	91A*	92	18.0	16.5-20.5	..	115
† <i>A. a. vittata</i> var. 1....	8	Meinecke, 1927-31	94A*	8	18.5	16.5-19.5	..	10
† <i>A. a. vittata</i> var. 1....	8	Meinecke, 1927-31	95A*	12	18.0	17.5-19.5	..	13
† <i>A. a. vittata</i> var. 2....	9	C. M. & R. A. Cooke	100-2*	53	18.5	16.5-21.5	..	75
† <i>A. a. cinerea</i> .....	10	C. M. Cooke	100B-13	32	19.0	16.5-20.5	..	92
† <i>A. a. cinerea</i> .....	10	C. M. Cooke	100B-12	17	19.5	18.5-20.5	..	36
† <i>A. a. cinerea</i> .....	10	Meinecke, 1911-16	100B-7?	7	19.0	17.5-20.5	..	25
<i>A. a. cinerea</i> .....	10?	Wilder, 50504	....	62	19.5	17.5-21.5	..	89
<i>A. a. cinerea</i> .....	10	R. A. Cooke, 58138	....	29	20.0	17.5-21.5	..	31
Region of ridge complex 3, zone II.								
<i>A. a. globosa</i> .....	?	All lots	....	20	17.5	16.5-18.5	23	..
Ridge complex 3, zone II.								
† <i>A. a. simulans</i> .....	16	Lemke	121-2	8	17.5	16.5-17.5	..	10
† <i>A. a. simulans</i> var. 1..	17	Lemke & Anderson	121, 121-1	10	17.0	15.5-17.5	..	17

†† For explanation of regions, ridge complexes, and zones, see pp. 189, 190, and 193, and fig. 8, p. 195.

† Used for plotting on map, fig. 8.

¶ Unless otherwise stated all catalog numbers are those of the Bishop Museum.

\* Asterisk indicates localities that were plotted from memory or prior to 1932.

? A question mark denotes there is some doubt concerning the correct plotting of a locality.

?? For two question marks, see explanation in text, p. 13.

TABLE 2.—Data on Material—Continued

Subspecies	Area	Collector¶	Locality	Adults	Mean length mm.	Length range mm.	Dex- tral	Sinis- tral
Ridge complex 3, zone III.								
† <i>A. a. vittata</i> .....	12	R. A. & C. M. Cooke, 58284, 22119	100E-1*	16	18.5	16.5-20.5	..	27
† <i>A. a. albofasciata</i> ....	13?	Wilder & Thurston	100A-1?	20	19.0	17.5-20.5	44	4
<i>A. a. albofasciata</i> var. 1	14??	J. S. Emerson	....	16	19.0	17.5-20.5	..	34
† <i>A. a. oliveri</i> .....	15?	O. H. & J. S. Emerson	120-1?	35	19.0	17.5-21.5	..	110
† <i>A. a. rubidipicta</i> .....	11	Meinecke, 1921	110*	119	19.5	16.5-21.5	..	166
† <i>A. a. rubidipicta</i> .....	11	Meinecke, 1922	110*	65	19.0	17.5-20.5	..	123
† <i>A. a. rubidipicta</i> .....	11	Meinecke, 1927	110*	76	19.5	16.5-21.5	..	100
† <i>A. a. rubidipicta</i> .....	11	Meinecke, 1929	110*	49	19.0	15.5-20.5	..	64
Ridge complex 4, zone II.								
† <i>A. a. simulans</i> var. 2..	19	Meinecke	151B*	12	18.5	16.5-19.5	..	33
Ridge complex 4, zone III.								
† <i>A. a. rubidipicta</i> var. 2.	18?	Wilder	Kahauiki	8	20.0	19.5-21.5	..	8
Ridge complex 4, probably zone III.								
<i>A. a. rubidipicta</i> var. 1.	?	Wilder	Kalihi	18	19.5	18.5-20.5	9	16
<i>A. a. rubidipicta</i> var. 3.	?	Wilder	Moanalua	75	19.5	17.5-21.5	..	93
REGION II.								
Ridge complex 5, zone II.								
† <i>A. a. ovum</i> var. 1.....	21	Meinecke	162B*	16	18.5	16.5-19.5	36	..
<i>A. a. ovum</i> var. 1.....	21?	Thurston	....	8	18.0	16.5-19.5	13	..
Ridge complex 5, zone III.								
† <i>A. a. ovum</i> .....	22	Meinecke	162C*	7	19.0	17.5-20.5	..	12
<i>A. a. ovum</i> .....	22?	Wilder, 50525	....	17	20.0	18.5-22.5	..	19
† <i>A. a. ovum</i> var. 2.....	23	Meinecke	162D*	22	19.5	17.5-20.5	..	33
† <i>A. a. ovum</i> var. 3.....	20	Meinecke & unlocal- ized J. S. & O. H. Emerson lots	163*	9	19.0	16.5-20.5	..	21
Ridge complex 6, zone II.								
† <i>A. a. pilsbryi</i> .....	26?	Cooke & Judd	170-1?	5	17.5	15.5-18.5	7	..
Ridge complex 6, zone III.								
<i>A. a. bruneola</i> var. 2..	25	Cooke & Judd	....	61	20.0	18.5-21.5	77	..
† <i>A. a. bruneola</i> var. 2..	25	Lemke	170C-6*	41	20.0	16.5-21.5	56	..
† <i>A. a. ovum</i> var. 2.....	24	Meinecke	174*	14	20.0	17.5-22.5	..	30
Ridge complex 7, zone II.								
† <i>A. a. laurani</i> .....	27	Meinecke	191*	7	18.5	17.5-19.5	..	17
† <i>A. a. laurani</i> .....	27A?	Cooke, Judd & Thurston	....	18	19.0	16.5-20.5	31	..
Ridge complex 7, zone III.								
† <i>A. a. bruneola</i> .....	28	Meinecke, 1926	182	9	19.0	17.5-20.5	12	..
† <i>A. a. bruneola</i> var. 1..	29	Meinecke, 1913	183?	19	20.0	18.5-22.5	2	32
† <i>A. a. bruneola</i> var. 1..	29	Meinecke, 1935	183	7	..	19.5-20.5	..	13
† <i>A. a. aureola</i> .....	30	Meinecke, 1913	184	12	20.5	19.5-22.5	1	47
† <i>A. a. aureola</i> .....	30	Meinecke, 1926	184	19	20.5	18.5-23.5	2	40
† <i>A. a. aureola</i> .....	30	Meinecke, 1932	187?	12	19.0	18.5-20.5	19	1
<i>A. a. aureola</i> .....	30	Meinecke, 1933	187	3	..	18.5-20.5	4	..
† <i>A. a. aureola</i> .....	30	Meinecke	185	10	20.0	18.5-21.5	..	16
† <i>A. a. aureola</i> var. 1..	31	Meinecke	190A*	10	18.5	17.5-20.5	17	..
Ridge complex 8, zone I.								
† <i>A. a. roseata</i> .....	37?	All lots	....	17	18.0	16.5-19.5	55	16
Ridge complex 8, zone II?								
† <i>A. a. parvicolor</i> .....	36??	Gulick	....	19	18.0	16.5-19.5	24	9



TABLE 2.—Data on Material—Continued

Subspecies	Area	Collector¶	Locality	Adults	Mean length	Length range	Dex- tral	Sinis- tral
					mm.	mm.		
Ridge complex 8, zone III.								
<i>A. a. turgida</i> .....	35	Meinecke, 1913	202B	15	18.5	17.5-19.5	12	19
† <i>A. a. turgida</i> .....	35	Meinecke, 1920	202B	31	19.0	17.5-21.5	35	15
† <i>A. a. turgida</i> .....	35	Meinecke, 1934	202B	9	19.0	16.5-20.5	15	2
<i>A. a. turgida</i> .....	35	Wilder, 50598	....	170	19.0	16.5-22.5	201	60
<i>A. a. turgida</i> .....	35?	J. S. Emerson, 102218	....	121	19.5	16.5-21.5	228	..
<i>A. a. turgida</i> .....	35?	J. S. Emerson, 102218	....	107	19.5	16.5-22.5	..	175
† <i>A. a. meadowsi</i> .....	34	Meinecke	212b	11	19.0	17.5-21.5	..	17
† <i>A. a. meadowsi</i> .....	34	Meinecke	213a	10	19.5	17.5-21.5	..	18
† <i>A. a. meadowsi</i> var. 2.	33	Meinecke	200Ca*	7	21.0	18.5-22.5	..	18
† <i>A. a. meadowsi</i> var. 2.	33	Meinecke	201C	5	21.5	20.5-22.5	..	11
† <i>A. a. waimaluensis</i> ...	32	Meinecke	202C	9	20.5	19.5-21.5	..	11
† <i>A. a. waimaluensis</i> ...	32	Meinecke	203C	7	20.0	18.5-20.5	..	14
REGIONS II?, IIIa.								
Ridge complex 9, zone II.								
† <i>A. a. perplexa</i> .....	40	Meinecke	222*	11	18.5	17.5-20.5	14	19
† <i>A. a. perplexa</i> .....	40	Meinecke	221½*	17	18.5	16.5-20.5	24	17
† <i>A. a. perplexa</i> .....	40?	Cooke	....	45	18.5	15.5-20.5	54	4
† <i>A. a. perplexa</i> .....	40?	Wilder	....	129	18.0	15.5-21.5	74	63
† <i>A. a. nigripicta</i> var. 1.	44?	Wilder	....	27	18.5	15.5-20.5	26	7
<i>A. a. nigripicta</i> var. 1.	44?	Cooke	....	23	17.5	16.5-19.5	41	1
<i>A. a. nigripicta</i> var. 1.	44?	J. S. Emerson, 10717	....	51	18.0	16.5-20.5	105	..
<i>A. a. nigripicta</i> var. 1.	44?	J. S. Emerson, 10718	....	110	19.0	16.5-22.5	..	201
<i>A. a. chromatacme</i>								
var. 1 .....	41	Meinecke	231*	68	18.5	16.5-20.5	13	102
† <i>A. a. chromatacme</i> .....	42	Meinecke	232	33	19.0	16.5-20.5	1	73
† <i>A. a. chromatacme</i> ...	42	Meinecke	234*	35	19.0	17.5-20.5	..	93
<i>A. a. chromatacme</i> ...	42	Meinecke	230B?	16	19.0	16.5-21.5	48	..
† <i>A. a. chromatacme</i> ...	42	Meinecke	235*	85	19.0	17.5-21.5	69	71
† <i>A. a. chromatacme</i> ...	42	Meinecke	236*	65	19.0	16.5-22.5	34	88
† <i>A. a. chromatacme</i>								
var. 2 .....	43	Meinecke	237*	23	18.5	16.5-21.5	49	2
Ridge complex 9, zone III.								
† <i>A. a. cookei</i> var. 1....	39	Meinecke	211B	7	19.0	17.5-20.5	..	27
<i>A. a. cookei</i> .....	45?	Wilder, 50594	....	116	19.0	17.5-21.5	..	142
<i>A. a. cookei</i> .....	45?	Wilder, 50595	....	12	19.0	17.5-20.5	13	..
<i>A. a. cookei</i> .....	45?	Baldwin & C. H. Cooke	....	8	20.0	18.5-21.5	12	..
<i>A. a. cookei</i> .....	45?	C. M. & R. A. Cooke	....	12	20.0	17.5-21.5	11	6
† <i>A. a. cookei</i> .....	45	Meinecke	226*	6	20.0	17.5-21.5	15	..
† <i>A. a. simulacrum</i> .....	46	Meinecke	228a	8	20.0	18.5-21.5	..	13
† <i>A. a. simulacrum</i> .....	46	Meinecke	228*	29	19.5	18.5-21.5	..	44
† <i>A. a. simulacrum</i> .....	46	Meinecke	229*	17	20.5	19.5-22.5	..	31
† <i>A. a. nigripicta</i> .....	50	Meinecke	237b	19	18.5	17.5-19.5	18	18
† <i>A. a. nigripicta</i> .....	50	Meinecke	237c	8	19.0	17.5-20.5	..	13
† <i>A. a. nigripicta</i> .....	50	Meinecke	237d	9	19.0	16.5-20.5	..	16
<i>A. a. nigripicta</i> .....	50	Thurston	....	65	19.0	16.5-20.5	27	62
† <i>A. a. cookei</i> var. 2....	49	Meinecke	237f	16	19.0	17.5-20.5	25	..
† <i>A. a. cookei</i> var. 2....	49	Meinecke	237fa	7	19.5	18.5-20.5	8	..
† <i>A. a. nigripicta</i> var. 2.	48	Meinecke	237h	13	19.5	18.5-20.5	22	..
† <i>A. a. nigripicta</i> var. 2.	48A	Meinecke	238a-238b	17	19.5	18.5-21.5	..	27
† <i>A. a. rubidilinea</i> .....	47	Meinecke	239a	7	20.5	18.5-21.5	..	8
† <i>A. a. rubidilinea</i> .....	47	Meinecke	220A?	11	19.5	18.5-21.5	..	22
REGION IIIa.								
Ridge complex 10, zone II.								
† <i>A. a. albipraetexta</i> ...	63?	Meinecke	231B*	22	18.0	16.5-20.5	..	45
† <i>A. a. albipraetexta</i> ...	63?	Meinecke	232B*	21	19.0	17.5-20.5	..	35
† <i>A. a. albipraetexta</i> ...	64	Lemke	233B-1*	14	19.0	16.5-20.5	13	6
Ridge complex 10, zone III.								
† <i>A. a. ewaensis</i> var. 1..	51	Meinecke	234B*	5	18.5	17.5-19.5	3	6

TABLE 2.—Data on Material—Continued

Subspecies	Area	Collector†	Locality	Adults	Mean length	Length range	Dex- tral	Sinis- tral
REGION III.								
Ridge complex 11, zone II.					mm.	mm.		
<i>A. a. griseibasis</i> .....	65??	J. S. & O. H. Emerson	....	21	17.5	15.5-20.5	46	1
<i>A. a. polymorpha</i> var. 1 .....	?	J. S. Emerson	....	15	18.0	16.5-19.5	18	5
† <i>A. a. flavitincta</i> .....	69	Meinecke	230G*	29	17.0	15.5-18.5	65	6
† <i>A. a. flavitincta</i> .....	69	Meinecke	231G?	23	17.0	15.5-17.5	32	..
† <i>A. a. flavitincta</i> .....	69	Meinecke	231G	41	17.0	15.5-17.5	64	12
<i>A. a. flavitincta</i> .....	69	Meinecke	232G*	47	16.5	15.5-18.5	17	80
† <i>A. a. lineipicta</i> .....	70	Meinecke	232Ga	17	17.0	15.5-18.5	..	20
<i>A. a. lineipicta</i> .....	70	Meinecke	233G*	9	18.5	17.5-20.5	16	..
† <i>A. a. lineipicta</i> .....	70	Meinecke	234G	25	17.0	15.5-18.5	33	1
† <i>A. a. lemkei</i> var. 1....	68?	Lemke	233Ga?	24	18.0	16.5-20.5	23	29
† <i>A. a. lemkei</i> .....	67?	Lemke	230E-1?	46	18.0	15.5-21.5	7	50
<i>A. a. fumositincta</i> ....	71	Meinecke	240*	13	17.5	16.5-19.5	..	46
† <i>A. a. fumositincta</i> ....	71	Welch	241-1*	8	16.5	15.5-17.5	..	27
† <i>A. a. fumositincta</i> ....	71	Russ	241-1?	8	16.5	15.5-17.5	1	10
† <i>A. a. fumositincta</i> ....	71	Russ	240-1-					
			241-1a?	11	16.5	15.5-17.5	2	13
† <i>A. a. fumositincta</i> ....	71	Welch	241-2*	15	17.0	15.5-18.5	1	44
† <i>A. a. fumositincta</i> ....	71	Welch	241-3*	6	16.5	15.5-17.5	..	17
Ridge complex 11, zone III.								
† <i>A. a. ewaensis</i> var. 3..	52	Meinecke	243-2*	9	18.5	16.5-19.5	12	4
† <i>A. a. ewaensis</i> var. 3..	52	Welch	243-4*	7	17.0	16.5-18.5	..	9
† <i>A. a. ewaensis</i> var. 2..	53	Meinecke	244*	15	16.5	15.5-18.5	..	33
† <i>A. a. ewaensis</i> var. 4..	54	Meinecke	244-3?	12	17.5	15.5-18.5	..	16
† <i>A. a. ewaensis</i> var. 4..	54	Meinecke	246*	7	17.5	16.5-19.5	..	13
Ridge complex 12, zone II.								
† <i>A. a. virgatifulva</i> ....	73?	Wilder	....	58	18.0	16.5-21.5	20	52
<i>A. a. virgatifulva</i> var. 2	74	Meinecke	250*	6	16.5	15.5-17.5	21	..
† <i>A. a. virgatifulva</i> var. 2	74?	Wilder, 50571	....	32	17.0	15.5-19.5	24	13
<i>A. a. virgatifulva</i> var. 2	74?	Wilder, 50573	....	32	17.5	14.5-20.5	23	13
Ridge complex 12, zone III.								
† <i>A. a. ewaensis</i> var. 5..	55	Meinecke	240L-1-1a	11	17.5	16.5-18.5	14	39
† <i>A. a. ewaensis</i> var. 5..	55	Meinecke	240L-1	11	17.5	15.5-19.5	..	17
† <i>A. a. ewaensis</i> .....	56	Meinecke	240L-4	11	17.5	16.5-18.5	12	4
† <i>A. a. ewaensis</i> .....	56	Meinecke	240L-6	7	17.5	15.5-18.5	9	..
† <i>A. a. ewaensis</i> var. 6..	57	Meinecke, 121935-121936	252-1-2?	29	16.5	15.5-17.5	25	24
† <i>A. a. ewaensis</i> var. 6..	57	Meinecke, 121937-121938	253?	31	17.0	15.5-18.5	28	15
† <i>A. a. ewaensis</i> var. 7..	58	Meinecke	256	7	17.0	16.5-18.5	..	15
† <i>A. a. ewaensis</i> var. 7..	58	Meinecke	257	18	18.0	15.5-20.5	18	11
Ridge complex 13, zone II.								
† <i>A. a. virgatifulva</i> var. 1	75?	Thurston, 130725	....	8	17.5	16.5-18.5	..	14
† <i>A. a. tuberans</i> var. 2..	60	Meinecke	261*	6	18.0	16.5-19.5	4	10
Ridge complex 13, zone III.								
† <i>A. a. ewaensis</i> var. 8..	59	Meinecke	261-262?	18	19.0	17.5-20.5	..	42
† <i>A. a. ewaensis</i> var. 8..	59?	Wilder	....	23	19.0	17.5-20.5	7	25
Portion of ridge complex 14, zone II.								
† <i>A. a. tuberans</i> var. 4..	76?	Meinecke, 1918	260A?	17	18.0	15.5-21.5	22	2
† <i>A. a. tuberans</i> var. 4..	76?	Meinecke, 1924	260A?	11	18.0	16.5-19.5	..	29
<i>A. a. tuberans</i> var. 4..	76?	O. H. Emerson	....	7	18.0	16.5-18.5	2	15
<i>A. a. tuberans</i> var. 4..	76?	Wilder	....	27	18.0	15.5-20.5	20	19
<i>A. a. tuberans</i> var. 5..	?	Wilder, 50575	....	56	16.5	15.5-18.5	60	15
<i>A. a. tuberans</i> var. 5..	?	L. A. Thurston	....	33	17.0	15.5-18.5	..	..

TABLE 2.—Data on Material—Continued

Subspecies	Area	Collector†	Locality	Adults	Mean length	Length range	Dex- tral	Sin- tral
REGION IV.								
Possibly in the region of ridge complexes 14, 15, zone I and lower zone II.								
					mm.	mm.		
<i>A. a. coniformis</i> .....	..	Gulick	Ahonui &					
			Kalaikoa	14	18.0	16.5-20.5	14	..
<i>A. a. coniformis</i> .....	..	Gulick	Wahiawa	23	17.5	16.5-20.5	28	3
<i>A. a. versicolor</i> .....	..	Gulick	Ahonui	14	17.0	14.5-18.5	..	56
<i>A. a. versicolor</i> .....	..	Gulick	Kalaikoa	12	17.0	15.5-19.5	..	28
<i>A. a. gulickii</i> .....	..	Gulick	Ahonui	8	18.0	16.5-18.5	19	9
<i>A. a. gulickii</i> var. 1....	..	Gulick	Ahonui	18	18.5	17.5-19.5	21	14
<i>A. a. gulickii</i> var. 2....	..	Gulick	Kalaikoa	8	16.5	15.5-18.5	10	17
<i>A. a. flavida</i> .....	..	Gulick	Ahonui &					
			Kalaikoa	8	16.5	15.5-17.5	47	5
Ridge complex 14, zone II.								
† <i>A. a. steeli</i> var. 1....	79	Wilder	....	18	19.0	17.5-20.5	26	..
† <i>A. a. steeli</i> .....	80	Russ	271	11	19.5	17.5-20.5	..	20
† <i>A. a. steeli</i> .....	80?	O. H. Emerson	....	19	19.5	17.5-21.5	..	34
† <i>A. a. steeli</i> .....	80?	Wilder, 50577	....	41	19.0	17.5-20.5	18	32
† <i>A. a. steeli</i> .....	80?	Wilder, 50580	....	13	19.0	17.5-20.5	..	16
<i>A. a. punicea</i> .....	81??	Wilder, 50581	....	6	19.0	17.5-20.5	3	4
† <i>A. a. punicea</i> .....	81??	Wilder, 50583	....	56	20.0	17.5-22.5	..	66
<i>A. a. punicea</i> var. 1....	82	Wilder, 50578	....	17	19.5	17.5-21.5	12	11
† <i>A. a. tuberosus</i> var. 3..	77	Lemke	274	15	19.5	17.5-21.5	19	..
<i>A. a. tuberosus</i> var. 3..	77	Wilder, 10448	....	7	19.0	18.5-20.5	9	1
Ridge complex 14, zone III.								
<i>A. a. irwini</i> .....	61?	Wilder	....	14	18.5	17.5-19.5	..	22
† <i>A. a. irwini</i> .....	61?	Meinecke	275?	13	19.0	17.5-21.5	4	14
† <i>A. a. irwini</i> var. 1....	62?	Meinecke, 1918	277?	45	18.0	16.5-20.5	..	60
† <i>A. a. irwini</i> var. 1....	62?	Meinecke, 1918	277?	13	19.0	17.5-20.5	19	..
† <i>A. a. irwini</i> var. 1....	62?	Meinecke, 1923	277?	10	18.5	16.5-20.5	5	13
Ridge complex 15, zone II.								
<i>A. a. lilacea</i> .....	*83b??	Gulick	Ahonui	17	19.0	17.5-20.5	25	..
<i>A. a. lilacea</i> .....	83b??	Gulick	Kalaikoa	14	19.0	17.5-20.5	21	..
† <i>A. a. lilacea</i> var. 1....	83	Meinecke	280*	18	18.5	16.5-20.5	57	..
† <i>A. a. lilacea</i> var. 1....	83	Russ	280-1-280*	27	18.5	16.5-20.5	37	..
<i>A. a. lilacea</i> var. 1....	83?	Wilder	....	23	18.5	17.5-19.5	14	11
† <i>A. a. lilacea</i> var. 1....	83a	Meinecke	281-2*	10	18.0	16.5-20.5	9	12
Ridge complex 15, zone III.								
† <i>A. a. lilacea</i> var. 2....	84	Meinecke	282-3	5	19.0	17.5-20.5	10	..
† <i>A. a. poamohonesis</i> ..	101	Meinecke	283-1-3-4	10	19.5	17.5-20.5	15	..
† <i>A. a. poamohonesis</i> ..	101	Meinecke	284-2	18	19.5	18.5-21.5	34	..
† <i>A. a. roseipicta</i> .....	102	Meinecke	285-3-286	32	19.0	17.5-19.5	55	..
<i>A. a. roseipicta</i> .....	102?	O. H. Emerson	....	29	19.0	17.5-21.5	39	..
<i>A. a. roseipicta</i> .....	102?	Wilder, 50563	....	55	19.0	16.5-21.5	65	..
† <i>A. a. roseipicta</i> var. 1.	103	Meinecke	287-1-3	18	19.5	18.5-20.5	30	..
† <i>A. a. roseipicta</i> var. 1.	103	Meinecke	288	6	20.0	18.5-21.5	10	..
† <i>A. a. roseipicta</i> var. 1.	103	Meinecke	289-1a	13	19.0	18.5-20.5	23	..
† <i>A. a. aloha</i> .....	100?	Wilder	....	169	19.0	17.5-24.5	191	..
† <i>A. a. aloha</i> .....	100?	Thurston	....	19	19.0	17.5-20.5	59	..
† <i>A. a. aloha</i> var. 1....	100?	Wilder	....	19	19.5	18.5-21.5	36	..
Possibly in the region of ridge complex 16, zone I or lower zone II.								
<i>A. a. apexalba</i> .....	..	Gulick	Ahonui	12	17.5	16.5-19.5	15	..
<i>A. a. apexalba</i> .....	..	Gulick	Wahiawa	31	17.0	14.5-19.5	26	62
<i>A. a. wahiawa</i> .....	..	Gulick	Wahiawa	15	17.5	16.5-18.5	38	3

\* See figure 7, page 194.

TABLE 2.—Data on Material—Continued

Subspecies	Area	Collector†	Locality	Adults	Mean length	Length range	Dex- tral	Sinis- tral
					mm.	mm.		
Ridge complex 16, zone II.								
† <i>A. a. suturafusca</i> ....	86	Meinecke	280K-1*	32	19.0	17.5-21.5	21	39
<i>A. a. suturafusca</i> ....	86?	Wilder	....	67	19.0	15.5-22.5	70	9
† <i>A. a. glaucopicta</i> ....	87	Meinecke	280K-2	10	19.0	15.5-20.5	14	9
† <i>A. a. brunosa</i> .....	88	Meinecke	280L-2	10	19.0	17.5-20.5	20	..
† <i>A. a. brunosa</i> .....	88	Meinecke	280L-4	9	18.5	17.5-20.5	..	13
† <i>A. a. suturalba</i> .....	90	Lemke	290AA-8	22	19.5	18.5-21.5	34	..
† <i>A. a. suturalba</i> .....	90	Welch	290AA-8	13	19.5	18.5-20.5	32	..
<i>A. a. suturalba</i> .....	90?	Wilder	....	44	19.0	16.5-21.5	58	..
† <i>A. a. suturafusca</i> var. 2	89	Meinecke, 1914	290*	57	19.5	17.5-21.5	102	7
† <i>A. a. suturafusca</i> var. 2	89	Meinecke, 1917	290*	63	19.0	17.5-21.5	11	72
<i>A. a. apicata</i> .....	92?	Gulick	Helemano	14	19.0	17.5-20.5	15	..
† <i>A. a. cervinivnea</i> ....	93	Russ	300-4*	17	19.5	18.5-20.5	17	..
<i>A. a. cervinivnea</i> ....	93	Meinecke, 1917	300-6	10	18.0	16.5-19.5	26	9
<i>A. a. cervinivnea</i> ....	93	Meinecke, 1916	300-6-301-2*	14	18.5	17.5-20.5	14	11
† <i>A. a. cervinivnea</i> ....	93?	Wilder, 50631	....	124	19.5	17.5-22.5	71	58
† <i>A. a. cervinivnea</i> ....	93?	Wilder, 50566	....	19	19.0	17.5-21.5	14	8
† <i>A. a. beata</i> var. 1.....	94	Meinecke, 1916	302*	19	19.0	16.5-20.5	25	6
† <i>A. a. beata</i> var. 1.....	94	Meinecke, 1932	302*	8	19.0	17.5-19.5	9	5
† <i>A. a. beata</i> var. 1.....	94	Meinecke, 1916-17	291-3-5*	33	19.0	17.5-21.5	69	..
† <i>A. a. beata</i> var. 1.....	94	Meinecke, 1932	291-3-5*	5	19.5	17.5-21.5	11	..
† <i>A. a. beata</i> var. 1.....	94?	Wilder, 50568-50569	....	59	19.0	17.5-20.5	88	3
† <i>A. a. beata</i> var. 1.....	94-94a?	Meinecke, 1914	291-2-302?	40	19.0	17.5-20.5	108	..
Ridge complex 16, zone III.								
† <i>A. a. beata</i> .....	104	Meinecke	280L-6	8	18.5	17.5-19.5	6	9
† <i>A. a. beata</i> .....	104	Meinecke	280L-9	15	20.0	18.5-21.5	18	..
† <i>A. a. beata</i> .....	104	Meinecke	303	8	19.5	18.5-21.5	11	..
† <i>A. a. beata</i> .....	104	Russ	303	17	19.5	17.5-21.5	21	1
† <i>A. a. beata</i> .....	104	Welch	304	7	19.5	18.5-21.5	11	..
<i>A. a. beata</i> .....	104	Meinecke, 1932	305-306?	11	19.0	18.5-20.5	26	..
<i>A. a. beata</i> .....	104	Meinecke, 1916	302-304?	9	19.0	17.5-20.5	18	..
<i>A. a. beata</i> .....	104?	Thurston	....	52	19.0	17.5-20.5	98	..
<i>A. a. beata</i> .....	104?	Wilder	....	75	19.5	18.5-21.5	91	..
<i>A. a. roseipicta</i> var. 2.	105	Meinecke	280L-2	8	20.0	18.5-21.5	12	..
† <i>A. a. roseipicta</i> var. 2.	105	Meinecke	307-3-308-1	8	19.5	18.5-20.5	15	..
† <i>A. a. roseipicta</i> var. 2.	105	Meinecke, 1917	307-1a-1b	20	19.0	17.5-20.5	47	..
<i>A. a. roseipicta</i> var. 2.	105	Lemke	307-3	13	20.0	18.5-21.5	17	..
† <i>A. a. roseipicta</i> var. 2.	105	Russ, 1932	308-1	7	19.0	17.5-21.5	8	..
Ridge complex 17, zone II.								
<i>A. a. suturalba</i> var. 1..	91??	J. S. Emerson	....	32	18.5	16.5-20.5	40	6
<i>A. a. suturalba</i> var. 1..	91??	Gulick	....	13	18.5	17.5-19.5	18	..
† <i>A. a. apicata</i> var. 1..	95	Meinecke, 1933	312-2-5	22	19.0	18.5-20.5	33	..
† <i>A. a. apicata</i> var. 1..	95	Meinecke, 1932	310-312-4*	30	19.5	16.5-22.5	71	1
† <i>A. a. paalaensis</i> .....	106	Meinecke	313-3	12	18.5	17.5-20.5	15	..
<i>A. a. apicata</i> var. 2...	96?	Wilder, 50510	....	89	19.0	16.5-22.5	113	2
Ridge complex 17, zone III.								
† <i>A. a. paalaensis</i> var. 1.	107	Meinecke	313-1	6	19.0	17.5-20.5	7	..
<i>A. a. paalaensis</i> var. 1.	107	Meinecke, 1932	314-1	12	18.5	17.5-19.5	31	..
† <i>A. a. paalaensis</i> var. 1.	107	Meinecke, 1933	314-1	10	20.0	18.5-21.5	14	..
† <i>A. a. paalaensis</i> var. 1.	107	Meinecke, 1932	316-1-3	27	19.5	18.5-21.5	33	..
† <i>A. a. paalaensis</i> var. 1.	107	Meinecke, 1933	316-1-3	19	19.5	18.5-20.5	37	..
† <i>A. a. paalaensis</i> var. 1.	107	Meinecke, 1932	334*	25	20.0	18.5-21.5	40	..
† <i>A. a. paalaensis</i> var. 1.	107	Meinecke	336-1*	7	19.5	17.5-20.5	13	..
<i>A. a. paalaensis</i> var. 1.	107	O. H. Emerson	....	22	19.5	17.5-20.5	57	..
† <i>A. a. beata</i> var. 2.....	108	Meinecke	318	37	19.5	18.5-21.5	67	..
† <i>A. a. beata</i> var. 2.....	108	Meinecke	318a	9	20.0	18.5-22.5	14	..
† <i>A. a. paalaensis</i> var. 2.	109	Meinecke, 1929	337-1-2?	12	20.0	18.5-22.5	16	..
† <i>A. a. paalaensis</i> var. 2.	109	Meinecke	337-3	9	20.0	18.5-20.5	14	..
<i>A. a. paalaensis</i> var. 2.	109	Meinecke, 1932	337-1-3?	15	19.5	18.5-20.5	28	..
<i>A. a. paalaensis</i> var. 2.	109	Meinecke, 1932	337-1-3?	15	19.5	17.5-21.5	29	..
<i>A. a. paalaensis</i> var. 2.	109	Meinecke, 1928	337-1-3?	12	19.5	17.5-21.5	17	..
† <i>A. a. beata</i> var. 3.....	110	Meinecke	337-4	13	19.5	17.5-20.5	26	..
<i>A. a. beata</i> var. 3.....	110	Meinecke	338-339-1?	26	19.5	17.5-21.5	46	..
† <i>A. a. beata</i> var. 3.....	110	Meinecke	338	6	20.5	19.5-22.5	16	..
† <i>A. a. beata</i> var. 3.....	110	Meinecke	339-1a*	15	20.0	18.5-21.5	30	..
<i>A. a. beata</i> var. 3.....	110	Meinecke	338?	6	20.0	18.5-21.5	16	..

TABLE 2.—Data on Material—Continued

Subspecies	Area	Collector¶	Locality	Adults	Mean length mm.	Length range mm.	Dex- tral	Sinis- tral
Ridge complex 18, zone I.								
† <i>A. a. duplocincta</i> .....	97A??	J. S. Emerson	....	56	18.0	16.5-19.5	61	..
Ridge complex 18, zone II.								
† <i>A. a. apexfulva</i> .....	97	J. S. Emerson	Opauala	37	18.5	17.5-19.5	38	..
Ridge complex 18, zone III.								
† <i>A. a. kawaiiki</i> .....	99?	Wilder & Thurston	....	9	19.5	16.5-20.5	16	..
† <i>A. a. vespertina</i> .....	98?	All lots	....	22	19.5	17.5-21.5	43	..
Somewhere between ridge complex 18 and 19, or in ridge complex 17 or 18.								
<i>A. a. bakeri</i> .....	..	J. S. Emerson & Judd	....	12	17.5	15.5-18.5	14	1
Probably ridge complex 19, zone I or lower zone II.								
<i>A. a. naps</i> .....	..	Gulick	....	10	18.5	16.5-20.5	16	..
<i>A. a. leucozona</i> .....	..	Gulick, ANSP 92656	....	78	17.5	15.5-19.5	164	..
<i>A. a. leucozona</i> .....	..	J. S. Emerson	....	8	17.5	16.5-18.5	10	..
Ridge complex 19, zone II.								
† <i>A. a. paumotuensis</i> ...	111	Meinecke	431	14	18.5	16.5-20.5	54	..
† <i>A. a. oioensis</i> .....	114	Meinecke	460A	9	17.5	16.5-18.5	13	..
† <i>A. a. oioensis</i> var. 2 ...	113	Meinecke	462*	21	18.5	16.5-19.5	56	..
<i>A. a. oioensis</i> var. 2 ...	113?	Thurston	....	23	17.5	16.5-19.5	37	..
† <i>A. a. oioensis</i> var. 1 ...	112	Meinecke	450	3	18.5	17.5-19.5	16	..
Ridge complex 20, zone I.								
† <i>A. a. wailensis</i> .....	117	Russ & Welch	....	14	18.5	15.5-20.5	57	..
Ridge complex 20, zone II.								
† <i>A. a. thiihiensis</i> .....	116	Welch	510-2a	5	18.0	16.5-19.5	10	..
Ridge complex 20, zone III.								
† <i>A. a. kahukuensis</i> ....	115?	Wilder & Thurston	....	22	19.5	17.5-21.5	55	..

## SPECIES CONCEPT

The species concept of *Achatinella apexfulva* is the same as that maintained for *A. mustelina* (Welch, 1938). If two forms are found in the same locality or in adjacent localities and are not found to hybridize they are considered distinct species. If hybrids are found between two forms A and B one is considered a subspecies of the other.

In the "Manual of Conchology" (1912-1914, p. 275) the various forms of *Achatinella* are divided into three large sections: Section *Bulimella* Pfeiffer, section *Achatinellastrum* Pfeiffer, and section *Achatinella* sensu strictu. The forms of the third section are divided by Cooke into eight species: *A. lorata*, *A. cestus*, *A. vittata*, *A. turgida*, *A. apexfulva*, *A. decora*, *A. valida*, and *A. mustelina*. Pilsbry added three more, *A. leucorraphe*, *A. swiftii*, and *A. concavospira*, making 11 species in all. However, Pilsbry states:

It was hoped that characters might be found in the reproductive organs which would aid to indicate specific boundaries, but dissections of *A. lorata*, *vittata similans*, and *mustelina* show no tangible structural differences.



A consistent arrangement of the species in linear order is impossible, as the group is formed of two parallel series which merge together in the less specialized median species of each.

The minor series consists of *apexfulva*, *turgida*, and *lorata*, species in which the apex is never black or dusky. These forms are confined to the Main range, but do not reach to either end.

In the greater series the tip of the apex is invariably dark in some species (*cestus*, *vittata*, *leucorraphe*), and is variable, either dusky or light, in others. The species are distributed over the whole length of both the main and the Waianae ranges.

An alternative and probably better grouping may be suggested. (1) Series of *lorata*, for *A. lorata*. (2) Series of *A. apexfulva*, for *A. apexfulva*, *turgida*, *saxifitii*, *leucorraphe*, *vittata*, *cestus*. (3) Series of *decora*, for *A. valida*, *decora*, *mustelina*, *concavospira*.

Since the publication of the Manual large collections of *Achatinella* from a great number of carefully plotted localities have been acquired for study by the Bishop Museum. These collections contain many hitherto unknown intermediate forms and greatly enlarge the species concept that resulted from the scant amount of material available in 1914. It is interesting to note that Pilsbry's alternative grouping of forms of *Achatinella* sensu strictu is almost the same as that derived from the study of additional material. The main difference is that instead of having species grouped under a series, each series is considered a single species, species complex, or Rassenkreise (Rensch, 1938) because intergrades for the most part are found existing between the various species.

In most places live specimens of *A. apexfulva* are comparatively rare. A general idea of the scarcity of the species can be obtained by looking at table 2 (p. 15). Most of the large lots were collected prior to 1932 by J. S. Emerson, Wilder, Cooke, Thurston, and Meinecke. In most cases they represent accumulations of shells acquired by numerous visits to the same place. The more recently collected Meinecke material consists mostly of small lots.

*Achatinella apexfulva* varies greatly in form and color pattern in different parts of the Koolau Range. Large sectors, however, produce no forms of *A. apexfulva*, the shells having either died out or escaped discovery. From Palolo to Pauoa Valleys (fig. 7, p. 194) there is a big gap in localities of *A. apexfulva*. But from Nuuanu to Opaepula Gulch a nearly complete series of forms is found from ridge to ridge, the forms more or less intergrading. Where a great deal of careful collecting has been done on certain ridges such as those from Waimano to Waiawa and those between South Kaukonahua Stream and Opaepula Gulch, certain areas are found to contain defi-

nite color forms at different elevations. Moreover, a color form belonging to a definite area is separated from the color form of another area by a region containing shells which have an intermediate color pattern or a mixture of the color patterns of the areas on either side of it. The extent of these intermediate localities has not yet been well determined, for the work in the Koolau Range is still in the pioneer stage because of the rareness of the shells, the roughness of the terrain, and the vast extent of the Koolau Range. The shells in a border region between two areas may have a color pattern which is a mixture of those of an upper and lower area and is also intermediate between those of the shells occurring on parallel ridges on either side of the area. From a study of the carefully collected regions of the Koolau Range and a study of the collection as a whole, so that the trend in the differentiation of *Achatinella* is determined, *Achatinella sensu strictu* is grouped into the following six species: 1, *A. lorata* Férussac; 2, *A. apexfulva* Dixon; 3, *A. turbini-formis* Gulick; 4, *A. concavospira* Pfeiffer; 5, *A. decora* Férussac; 6, *A. mustelina* Mighels. This paper concerns only *A. apexfulva*; a discussion of species 1, 3, 4, and 5 will be reserved for future papers.

Subspecific groups will be used in this paper to group together the lower orders of forms of *A. apexfulva*, as is done for *A. mustelina* (Welch, 1938). The term "variety" will also denote that a particular form is closely related to a particular subspecies but has not enough distinctive characters to warrant its separation into a definite subspecies. All varieties will be numbered var. 1, var. 2, etc.

## TAXONOMY

### SYNOPSIS OF THE SUBSPECIES OF ACHATINELLA APEXFULVA DIXON

The following synopsis is purely an artificial grouping of forms that seem to be similar. No great detail will be attempted because so few really distinct characters exist beyond the shape and color of the embryonic whorls and size of the shells. The color pattern of the postembryonic whorls in some regions is of use, but very often it is of little aid since the same pattern may occur again and again in widely separated forms. Unless otherwise stated the color pattern of the shell is the color of the last two postembryonic whorls.

A. Embryonic whorls bicolored. First embryonic whorl a dark color (black, gray, light brown), remaining embryonic whorls white, cream buff, or some shade of yellowish white. The dark band or line usually fades out, on the first quarter or first half of the second embryonic whorl, into the ground color or into a light yellowish-white band or

line at the lower edge of the whorl, which finally may fade out entirely on the last quarter whorl.

a. Embryonic whorls pointed. First embryonic whorl light reddish brown (pecan brown, army brown, walnut brown, sepia), remaining embryonic whorls usually white. Exceptions are *A. a. buena*, *A. a. cinerea*, and *A. a. hanleyana*, which have yellow or yellow-banded embryonic whorls (such as pinkish buff, tilleul buff, cinnamon buff).

I. Small usually lowland forms, occurring mostly in zone II,<sup>1</sup> regions I, Ia, which may be white or buff, lined, banded, streaked, or spotted with brown or reddish brown, or the patterns may be gray or gray brown. The mean length ranges from 15.5 to 20.5 mm.

Group of *A. a. cestus* Newcomb

1. *A. a. muricolor*, new subspecies
2. *A. a. waialaeensis*, new subspecies
3. *A. a. forbesiana* Pfeiffer
4. *A. a. fuscostriata*, new subspecies
5. *A. a. innotabilis* Smith
6. *A. a. cestus* Newcomb
7. *A. a. simulator* Pilsbry and Cooke
8. *A. a. buena*, new subspecies
9. *A. a. globosa* Pfeiffer
10. *A. a. hanleyana* Pfeiffer
11. *A. a. simulans* Reeve

II. White obese forms lined with reddish brown having a mean length of 18.5 to 20.5 mm., and occurring in zone III, regions I, Ia. They are larger than shells belonging to the group of *A. a. cestus*.

Group of *A. a. vittata* Reeve

1. *A. a. vittata* Reeve
2. *A. a. cinerea* Sykes
3. *A. a. albofasciata* Smith
4. *A. a. oliveri*, new subspecies
5. *A. a. rubidipicta*, new subspecies

b. Embryonic whorls blunt, usually banded with yellow. Forms occurring between North Waiawa Stream and the upper portion of the North-South Kaukonahua Ridge.

I. The color pattern may have the white ground tinted or banded with buff or gray, or the ground may be buff or a light shade of gray. The shell is usually lined or banded with gray, reddish brown, or

<sup>1</sup> For discussion of zones and regions see pp. 189, 190, and figs. 7, 8, pp. 194, 195.



brown and is found in zone II, region III, from Waiawa to Kipapa Gulch.....Group of *A. a. polymorpha* Gulick

1. *A. a. polymorpha* Gulick
2. *A. a. flavitincta*, new subspecies
3. *A. a. lemkei*, new subspecies
4. *A. a. lineipicta*, new subspecies
5. *A. a. fumositincta*, new subspecies

*Note.*—Some specimens of *A. a. polymorpha* and its varieties lack the dark color, such as black or gray, on the first embryonic whorl.

II. The pattern is a strongly axially streaked one, the color brownish gray or light tan, impressed sutural band white, brown, or buff. The forms are limited to zone II, region III, between Kipapa Gulch and South Kaukonahua Stream. Exception, *A. a. tubersans*, which has banded forms that may or may not be strongly axially streaked.

Group of *A. a. leucorraphe* Gulick

1. *A. a. virgatifulva*, new subspecies
2. *A. a. leucorraphe* Gulick
3. *A. a. tubersans* Gulick

III. White shells lined or banded with reddish brown, gray, and sometimes yellow occurring in zone III, region III.

Group of *A. a. irwini* Pilsbry and Cooke

1. *A. a. ewaensis*, new subspecies
2. *A. a. irwini* Pilsbry and Cooke

B. Embryonic whorls unicolored.

a. Embryonic whorls white.

I. Embryonic whorls very pointed to moderately pointed. Small shells from the lowland zone or zones I and II, region II; mean length from 17.5 to 18.5 mm.. Group of *A. a. pilsbryi*, new subspecies

1. *A. a. pilsbryi*, new subspecies
2. *A. a. roseata*, new subspecies
3. *A. a. laurani*, new subspecies
4. *A. a. parvicolor*, new subspecies

*A. a. laurani* and *A. a. parvicolor* are intermediate forms between a lower smaller race with very pointed embryonic whorls, occurring in lower zone I, and a large obese race of shells inhabiting an upper zone or zone III. I am merely putting them in the subspecific group of *A. a. pilsbryi* because they are closer to the form of *pilsbryi* than to the upper group of *A. a. turgida*.

II. Large obese shells found mostly in zone III, region II, and zone II, region IIIa, between Moanalua and Waiawa Streams. Embryonic whorls moderately pointed, usually white but sometimes cream buff; mean length, 18.5 to 21.5 mm.

Group of *A. a. turgida* Newcomb

1. *A. a. ovum* Pfeiffer
2. *A. a. bruneola*, new subspecies
3. *A. a. aureola*, new subspecies
4. *A. a. waimaluensis*, new subspecies
5. *A. a. turgida* Newcomb
6. *A. a. meadowsi*, new subspecies
7. *A. a. perplexa* Pilsbry and Cooke
8. *A. a. nigripicta*, new subspecies
9. *A. a. cookei* Baldwin
10. *A. a. simulacrum* Pilsbry and Cooke
11. *A. a. rubidilinea*, new subspecies
12. *A. a. chromatacme* Pilsbry and Cooke
13. *A. a. griseibasis*, new subspecies
14. *A. a. albipraetexta*, new subspecies

*Note.*—*A. a. chromatacme* differs from the remaining subspecies of this group in having shells with darker embryonic whorls of tan or yellowish brown. *A. a. griseibasis* has more loosely coiled embryonic whorls which are intermediate between the embryonic whorls of the groups of *A. a. turgida* and *A. a. leucorraphe*.

b. Embryonic whorls white in a few forms, but usually they are tinted with buff or yellow, or are a deep shade of yellow or yellowish brown.

I. Small shells probably from zone I or lower zone II, region IV, between South Kaukonahua Stream and North Helemano Stream. All forms extinct as far as is known. Gray or gray-brown lined or streaked color patterns, embryonic whorls white or tinted cream color.

Group of *A. a. coniformis* Gulick

1. *A. a. coniformis* Gulick
2. *A. a. apexalba*, new subspecies
3. *A. a. versicolor* Gulick
4. *A. a. wahiawa*, new subspecies

II. Shells with color patterns of light pastel shades of pink, yellow, deep cream, or blue gray, usually lightly axially streaked with similar colors darker than the ground color. They occur in zone II and probably zone I, region IV, between South Kaukonahua Stream and

North Kaukonahua Stream. Exceptions are *A. a. steeli*, *A. a. gulickii*, which are banded with reddish brown or dark gray and strongly axially streaked; *A. a. flavidus*, which may lack streaking or may be banded with brown. . . . . Group of *A. a. lilacea* Gulick

1. *A. a. gulickii* Smith
2. *A. a. flavida* Gulick
3. *A. a. lilacea* Gulick
4. *A. a. glaucopicta*, new subspecies
5. *A. a. punicea*, new subspecies
6. *A. a. steeli*, new subspecies

III. Strongly axially streaked brown and gray color forms from zone II and the lower part of zone III, region IV, between Poamoho Stream and Kawainui Gulch. Embryonic whorls usually a dark yellowish brown. Exceptions are *A. a. brunosa* and *A. a. kawaiiki*, which have lighter embryonic whorls. . . . . Group of *A. a. apicata* Newcomb

1. *A. a. brunosa*, new subspecies
2. *A. a. suturafusca*, new subspecies
3. *A. a. suturalba*, new subspecies
4. *A. a. apicata* Newcomb
5. *A. a. paalaensis*, new subspecies
6. *A. a. kawaiiki*, new subspecies

IV. Not markedly axially streaked, white or light color patterns. The color is mostly light pink, light gray, flesh tints, usually banded over white or colors almost solid on the last two whorls. Exceptions are the dark gray color pattern of *A. a. cervixnivea*, the reddish-brown pattern of *A. a. beata*, which may resemble typical *apexfulva*, and also *A. a. kahukuensis* which has a white spire and a yellow base. These forms inhabit zone III and the upper part of zone II, region IV, from North Kaukonahua Stream to the Malaekahana-Kaluakauila Ridge. . . . . Group of *A. a. aloha* Pilsbry and Cooke

1. *A. a. aloha* Pilsbry and Cooke
2. *A. a. roseipicta*, new subspecies
3. *A. a. poamohoensis*, new subspecies
4. *A. a. cervixnivea* Pilsbry and Cooke
5. *A. a. beata* Pilsbry and Cooke
6. *A. a. vespertina* Baldwin
7. *A. a. kahukuensis* Pilsbry and Cooke

V. Small lowland forms from zones I and II, region IV, northwest of Helemano Stream. Embryonic whorls white, cream, or yellow. Mean length, 16.5 to 18.5 mm.

Group *A. a. apexfulva* Dixon

1. *A. a. apexfulva* Dixon
2. *A. a. duplocincta* Pilsbry and Cooke
3. *A. a. bakeri*, new subspecies
4. *A. a. naps* Pfeiffer
5. *A. a. leucozona* Gulick
6. *A. a. paumaluensis*, new subspecies
7. *A. a. oioensis*, new subspecies
8. *A. a. ihiihiensis*, new subspecies
9. *A. a. wailelensis*, new subspecies

#### GROUP OF *A. a. CESTUS* NEWCOMB

#### **ACHATINELLA APEXFULVA FORBESIANA** Pfeiffer

PLATE I, FIGURE 2; PLATE 4, FIGURES 5-6a

*Achatinella forbesiana* PFEIFFER, Proc. Zool. Soc. London, 1855, p. 5, pl. 30, fig. 16.

*Achatinella cestus* NEWCOMB, Pilsbry and Cooke, Man. Conch., vol. 22, pp. 286, 288, pl. 52, figs. 11-11b, 13 (only), 1914.

The last two whorls are usually brown, lined with white; banded with a white band at the edge of the periphery of the last whorl; embryonic whorls pointed and bicolored.

The last two whorls of the lectotype (pl. 4, fig. 5) are lined with white; penultimate vinaceous drab, last whorl vandyke brown and rood's brown, peripheral band white; lip and columella callus vinaceous buff. Length 18.4 mm., greater diameter 11.2 mm., spire height 9.3 mm., number of whorls  $6\frac{1}{2}$ .

Distribution, area 6??: **Waialae**, Gulick. The race probably occurred at a low elevation in either **Waialae Nui** or **Waialae Iki Gulch** (fig. 3a, p. 29). Gulick also reports it from Wailupe, but this may be an error due to mixture of material from different localities. Lectotype in BM.

The usual form is sinistral (pl. 1, fig. 2); postembryonic whorls pale pinkish cinnamon, streaked with sorghum brown and pale mouse gray, last two whorls lined with pale pinkish cinnamon and white, peripheral band white; lip cinnamon; impressed sutural band cinnamon buff. Length 16.9 mm., greater diameter 11.0 mm., spire height 9.0 mm., number of whorls 6.

A dextral shell (pl. 4, fig. 6) has a light gray color pattern; postembryonic whorls pale smoke gray darkening to ecru drab on the last whorl, last whorl and a half lined and banded with white. Length 17.8 mm., greater diameter 11.3 mm., spire height 9.5 mm. A narrow dextral (pl. 4, fig. 6a) measures: Length 17.3 mm., greater diameter 10.5 mm., spire height 10.0 mm.; color pattern similar to plate 1, figure 2.

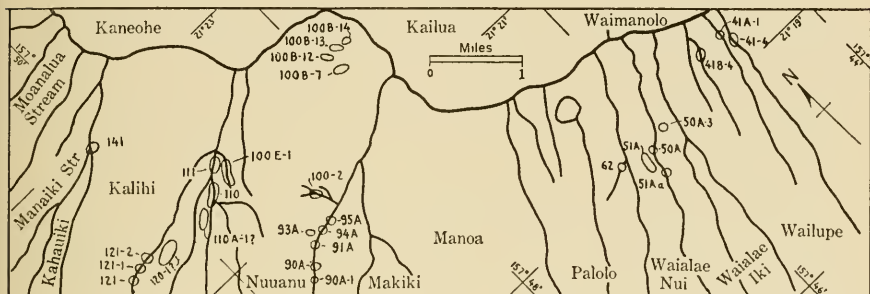


FIG. 3.—Eastern Oahu, leeward slope of the Koolau Range, including region I (fig. 7, p. 194), showing localities of subspecies of *A. apexfulva* belonging to the groups of *A. a. cestus* and *A. a. vittata*.

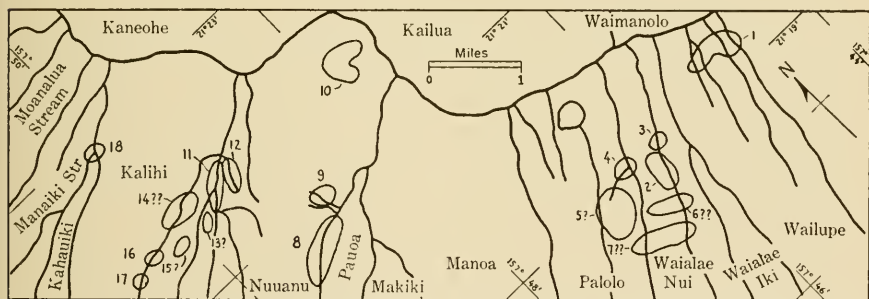


FIG. 3a.—Same as fig. 3, but exhibiting the area occupied by different subspecies of *A. apexfulva* belonging to the groups of *A. a. cestus* and *A. a. vittata*.

#### ACHATINELLA APEXFULVA WAIALAEENSIS, new subspecies

'PLATE I, FIGURE 3; PLATE 4, FIGURES 2-4

This race has a characteristic axially streaked color pattern, and lacks the spiral lines and bands of *A. a. forbesiana*, although it has the white peripheral band on the last whorl. *A. a. forbesiana* is an extinct race which probably existed at a low elevation immediately below the area occupied by *A. a. waialaeensis*.

The holotype of *A. a. waialaeensis* (pl. 1, fig. 3) has the first fourth postembryonic whorl mikado brown, remainder of the first



postembryonic whorl and penultimate whorl drab gray axially streaked with benzo brown, the first half of the last whorl is drab axially streaked with bone brown, tinted below the tawny impressed sutural band with tawny, last half whorl changes from drab to tawny axially streaked with bone brown, peripheral band white; lip and columella callus army brown. Length 18.8 mm., greater diameter 11.5 mm., spire 10.5 mm., number of whorls  $6\frac{1}{4}$ .

Distribution, area 2: **Waialae Iki-Waialae Nui Ridge**, type locality 51Aa, elevation 1,250-1,350 feet, Meinecke, 1933; also 51A\*, elevation 1,000-1,350 feet, Meinecke, 6 sinistral 1926, 1 sinistral 1928; **Waialae Nui Gulch**, locality 50A\*, elevation 1,400-1,450 feet, Meinecke 1926, 1 sinistral 1929. Also collected in the region of **Waialae Iki-Waialae Nui Ridge** by O. H. Emerson, BBM 103924, 1916, BBM 103926, 7 sinistral 1918; **Waialae**, Wailupe, Gulick.

Area 3: **Waialae Iki-Waialae Nui Ridge**, locality 50A-3, elevation 1,500-1,650 feet, O. H. Emerson, BBM 167275-167276, 6 sinistral 1937 (figs. 3, 3a, p. 29).

The lightest color pattern (pl. 4, fig. 2) is gray; postembryonic whorls pale ecru drab streaked with drab gray and ecru drab, tinted on the last half whorl with sayal brown, and streaked with verona brown, impressed sutural band mikado brown.

Plate 4, figures 2a and 3, show reddish-brown patterns of this race which are peculiar to the shells of Waialae. The shell of figure 2a has dark vinaceous brown postembryonic whorls streaked with drab gray or deep olive buff. That of figure 3 has mikado brown postembryonic whorls darkening to cameo brown on the last whorl, at the edge of the periphery a band of cinnamon buff.

In locality 50A-3 only dextrals occur. The typical form (pl. 4, fig. 4) has the last two postembryonic whorls pinkish buff axially streaked with saccardo's umber and sepia, last half whorl snuff brown. Length 18.2 mm., greater diameter 12.0 mm., spire height 9.6 mm.

#### **ACHATINELLA APEXFULVA MURICOLOR**, new subspecies

PLATE 1, FIGURE 1; PLATE 4, FIGURES 1-1b

*Achatinella cestus* NEWCOMB, Pilsbry and Cooke, Man. Conch., vol. 22, p. 288, pl. 52, figs. 9, 9a, 10 (only), 1914.

The shell resembles *A. a. waialaensis* but differs in having the dominant pattern always profusely lined with white over a gray ground. No reddish-brown color forms occur in this race and the characteristic white peripheral band is usually lacking, but may be present.

The postembryonic whorls of the holotype (pl. 1, fig. 1) are drab gray shading to drab, axially streaked on the last two whorls with snuff brown and bister, spirally lined with white; impressed sutural band cinnamon; lip and columella callus fawn color. Length 17.3 mm., greater diameter 11.1 mm., spire height 9.3 mm., number of whorls 6.

Distribution, area 1: **Niu-Wailupe Ridge**, type locality 41-4\*, elevation 1,650-1,750 feet, Meinecke, BBM 120184, 120177, 1926, also BBM 120197, 6 sinistral 1931; **Kului-Laulaupoe Ridge, Wailupe**, locality 41A-1\*, elevation 1,800-2,000 feet, Meinecke, BBM 120216-120217, 1926; **Laulaupoe-Wailupe Ridge, Wailupe**, 41B-4\*, elevation 1,950-2,000 feet, Meinecke, BBM 120225, 1926 (figs. 3, 3a, p. 29).

The lightest color form of the shell (pl. 4, fig. 1) has the postembryonic whorls pale drab gray axially streaked with light drab; impressed sutural band pale pinkish cinnamon streaked with light pinkish cinnamon; last whorl lined with white. This color pattern resembles the light color pattern of *A. a. zwaialacensis* (pl. 4, fig. 2), but *muricolor* is definitely more lined and lacks the strong white peripheral band. An obese shell (pl. 4, fig. 1a) measures: Length 17.3 mm., greater diameter 11.8 mm., spire height 8.6 mm.; the postembryonic whorls strongly lined, last two whorls lilac buff lined and banded with wood brown, natal brown, snuff brown, and bister, peripheral band white; lip and columella callus wood brown.

A rare dark color pattern (pl. 4, fig. 1b) occurs on 7 specimens out of a total of 194 taken at various times from locality 41-4. The last two whorls are drab lightly axially streaked with vinaceous and sepia, faintly lined with pale pinkish buff.

#### ACHATINELLA APEXFULVA CESTUS Newcomb

PLATE 1, FIGURE 5; PLATE 4, FIGURES 9-11

*Achatinella cestus* NEWCOMB, Proc. Zool. Soc. London, 1853, p. 132, pl. 22, fig. 8.—PILSBRY and COOKE, Man. Conch., vol. 22, p. 286, pl. 29, fig. 8; pl. 55, fig. 1 (only), 1914.

This form is characterized by having a light yellowish-white ground splotted or rarely banded on the last two whorls above the periphery with reddish brown, and by having a dark reddish-brown band below the periphery; the base may be banded or splotted with reddish brown.

The lectotype (pl. 4, fig. 9) is marked with an "x" by me. The last two whorls are white streaked with splottches of walnut brown and

chocolate, below the periphery a band of chocolate and a band of white; lip and columella callus light brownish vinaceous. Length 17.7 mm., greater diameter 11.6 mm., spire height 9.6 mm., number of whorls 6.

Distribution, area 5?: Palolo, Gulick; Waiomao Stream, Palolo, Spalding, somewhere in the region of area 5? (figs. 3, 3a, p. 29). Gulick also reports specimens from Wailupe and Waialae, but I believe these are errors due to a mixture, because the known highland forms of this group from Waialae have distinctly different patterns from those of Palolo, and the lowland forms, if not extinct today, most probably would show a similar variation. Also collected by D. D. Baldwin, BBM 54741. Lectotype BM.

The Spalding lot contains only specimens of *A. a. cestus* and no specimens of *A. a. fuscostriata*, with which form *A. a. cestus* is always mixed in the Gulick collection. Pilsbry (Pilsbry and Cooke, 1912-1914, p. 287) mentions the fact that the Spalding lot contains dextral specimens of *A. a. simulator* which are undoubtedly *A. a. simulator* var. 1 of area 4. Judging from the data at hand, I believe that *cestus* is a distinct race from *A. a. fuscostriata* and probably grades into the higher race of *A. a. simulator* var. 1.

Specimen A of the BM type lot (pl. 4, fig. 10) has the white ground of the last whorl above the periphery streaked with zigzag lines and axial streaks of chocolate, below the periphery banded with chocolate and white.

In one BBM lot labeled Wailupe (pl. 4, fig. 11) a light color pattern has the postembryonic whorls pale pinkish cinnamon, lightly streaked with avellaneous, below the periphery of the last whorl a band of russet and a band of buckthorn brown.

A sinistral (pl. 1, fig. 5) resembles the lectotype; postembryonic whorls pale pinkish buff, splotted and streaked with russet, at the edge of the periphery a band of white, below the periphery a band of russet, a band of white, and a line of tawny.

#### **ACHATINELLA APEXFULVA FUSCOSTRIATA, new subspecies**

PLATE 1, FIGURE 4; PLATE 4, FIGURES 7, 7a

*Achatinella cestus* NEWCOMB, Pilsbry and Cooke, Man. Conch., vol. 22, pp. 287, 288, pl. 52, figs. 12, 12a, 13a, 14, 14a (only), 1914.

This extinct form resembles *A. a. cestus* but differs in not having the characteristic dark reddish-brown subperipheral band. The ground color is usually darker, being a yellowish cream instead of the white or whitish cream color of *A. a. cestus*. Both forms have a



zigzag pattern and probably came from adjacent areas. Possibly *fuscostriata* came from some area below *A. a. cestus* in Palolo or Waialae Nui somewhere in the region of area 7??.

The postembryonic whorls of the holotype (pl. 1, fig. 4) are pinkish buff axially streaked with straight and zigzag lines of russet, last whorl with a white peripheral band, base banded with white and carob brown; lip and columella callus avellaneous. Length 16.4 mm., greater diameter 11.2 mm., spire height 8.4 mm., number of whorls 6.

Distribution, area 7??: Type locality **Palolo**, Gulick; also **Waialae**, Wailupe, Gulick (fig. 3a, p. 29). So much of the Gulick material is undoubtedly mixed from several valleys that the true distribution of the lowland races of *Achatinella* cannot be worked out from his data, if all his labels are considered correct. I do not believe this form ever occurred in Wailupe.

The color pattern may lack a white peripheral band on the last whorl (pl. 4, fig. 7), postembryonic whorls pale pinkish buff streaked with cinnamon, base banded with white. A dextral specimen (pl. 4, fig. 7a) has the postembryonic whorls cream buff, axially streaked with cinnamon, the last whorl banded above and below the edge of the periphery with a band made up of broken lines of cinnamon, basal band white and pinkish cinnamon.

#### ACHATINELLA APEXFULVA INNOTABILIS Smith

##### PLATE 4, FIGURE 8

*Apex innotabilis* SMITH, Proc. Zool. Soc. London, 1873, p. 78, pl. 9, fig. 23 (not fig. 19).

*Achatinella swiftii* NEWCOMB, Pilsbry and Cooke, Man. Conch., vol. 22, pp. 306, 309, pl. 59, fig. 7 (only), 1914.

The holotype in the British Museum is marked with a red spot of sealing wax. The embryonic whorls are similar to *A. a. cestus*; postembryonic whorls are light pinkish cinnamon axially streaked with a darker shade of the ground color, peripheral band pale pinkish buff; lip pale pinkish buff; columella callus white. Length 18.1 mm., greater diameter 12.0 mm., spire height 10.6 mm., number of whorls 6.

This color form is undoubtedly a distinct race which is now extinct. Specimens of *A. a. innotabilis* are rare and are found only in collections made prior to 1900. The form is closest to that of *A. a. fuscostriata*. It was possibly a lowland race occurring below or near *fuscostriata*. *A. a. fuscostriata* may be an intermediate race between *A. a. innotabilis* and *A. a. cestus*. *A. a. innotabilis* possibly occurred in Wailupe.

**ACHATINELLA APEXFULVA SIMULATOR** Pilsbry and Cooke

PLATE 1, FIGURE 6; PLATE 4, FIGURES 12-13a

*Achatinella cestus* color form *simulator* PILSBRY and COOKE, Man. Conch., vol. 22, p. 287, pl. 55, figs. 2, 3, 4, 1914.

The holotype of *A. a. simulator* selected by Pilsbry and myself is figured in the Manual of Conchology (pl. 55, fig. 2) and illustrated in this paper on plate 4, figure 12. The postembryonic whorls are white lined with chocolate except for a line of pecan brown on the last whorl below the suture; sutural band white. Length 17.8 mm., greater diameter 12.2 mm., number of whorls 6.

Distribution, area?: **Palolo**, Gulick. Pilsbry (Pilsbry and Cooke, 1912-1914, p. 287), says: "A small lot; No. 42 coll. Irwin Spalding, consists of dextral shells which occurred with the typical color form of *cestus*." This form is not typical *simulator* but is what I consider to be *A. a. simulator* var. 1. Typical *simulator* is a lowland race now extinct.

The color pattern of the holotype is a rare one occurring on only one specimen in the Gulick lots in the Bishop Museum. The usual color pattern and form of the shell (pl. 1, fig. 6) has white postembryonic whorls, lined on the last whorl with pinkish cinnamon, about the base a band of cinnamon; lip pale cinnamon pink slightly corrugated or roughened. Length 17.4 mm., greater diameter 11.5 mm., spire height 9.2 mm., number of whorls 6.

The shell may be more obese (pl. 4, fig. 13), length 17.2 mm., greater diameter 12.3 mm., spire height 8.5 mm., last whorl lined with cinnamon about the periphery, and army brown about the base. Dextral forms were also found by Gulick. A dextral specimen is figured on plate 4, figure 13a.

**ACHATINELLA APEXFULVA SIMULATOR** var. 1

PLATE 1, FIGURE 7

Area 4: **Waiomao Stream, Palolo**, locality 62, elevation 1,250-1,350 feet, Meinecke, 8 dextral 1933, and 13 dextral 1914 (figs. 3, 3a, p. 29).

The shell is very close to *A. a. simulator* and differs only in the arrangement of the bands. Typical *A. a. simulator* always has a line or band at the edge of the periphery, and the bands and lines are never broken by axial streaks of a lighter color. The typical form of this variety (pl. 1, fig. 7) has white postembryonic whorls, last whorl above the periphery with a faint band of tilleul buff, below the periphery the last whorl banded with mikado brown, which bands

are streaked with white, in the umbilical region a band of naples yellow; lip and columella callus light vinaceous fawn. Length 17.0 mm., greater diameter 11.8 mm., spire height 9.2 mm., number of whorls 6.

**ACHATINELLA APEXFULVA BUENA, new subspecies**

PLATE I, FIGURE 8; PLATE 4, FIGURES 14, 14a

The shell is small, sinistral, and seems to be closest in form to *A. a. simulator* but may be a race which occurred near *A. a. hanleyana*. The yellow-banded embryonic whorls are different from anything known from the region of Wailupe to Kalihi Valleys. However, because of the darkened embryonic whorls and the small size of the shells, this distinct color form is placed under the subspecific group of *A. a. cestus*. The first embryonic whorl of the holotype (pl. 1, fig. 8) is army brown, next whorl, upper eighth white, lower seven-eighths shades from avellaneous to chamois, last embryonic whorl, upper half white, lower half chamois; postembryonic whorls white banded just above the edge of the periphery with a band of russet flecked with light buff, on last whorl suprapерipheral band not so intense, having more streaks and flecks of light buff in it, peripheral band white except for a line of tawny on the lower portion of the band, base tawny axially streaked with light buff, with a line of white and a band of cream color in the umbilical region; lip and columella callus vinaceous buff. Length 16.4 mm., greater diameter 10.6 mm., spire height 8.8 mm., number of whorls  $5\frac{3}{4}$ .

This subspecies has been named after Buena Blok, the wife of Arthur Blok, of London, an ardent student of conchology.

Distribution, area?: **Nuuanu, west side, J. S. Emerson, BBM 102185, 33302.**

This form appears in the Gulick collection in several lots. In one lot from Palolo one specimen is found mixed with *A. a. simulator*. Gulick has another lot labeled Waipio BBM 70382, and still another Kalaikoa BBM 106736. It is probable that the Emerson and Gulick shells all came from a single now extinct lowland locality, but the exact location is not known. Another specimen was obtained from A. Block, BBM 165793, and one from Sowerby and Fulton, BBM 165794.

A narrow specimen (pl. 4, fig. 14) measures: Length 16.6 mm., greater diameter 10.0 mm., spire height 8.9 mm.; the postembryonic whorls are more heavily banded than the type, the bands are wood brown flecked with vinaceous buff. A light color form (pl. 4, fig. 14a)

has the postembryonic whorls white, banded on the penultimate above the periphery with a narrow band of russet, last whorl lined just above the periphery with a line of tawny, below the periphery ground white tinted with cream color, base banded with tawny and lined with cream color.

**ACHATINELLA APEXFULVA GLOBOSA Pfeiffer**

PLATE 1, FIGURE 12; PLATE 4, FIGURES 21-24

*Achatinella globosa* PFEIFFER, Proc. Zool. Soc. London, 1855, p. 7, pl. 30, fig. 25.  
*Achatinella vittata* REEVE, Pilsbry and Cooke, Man. Conch., vol. 22, pp. 289-291, pl. 30, fig. 25; pl. 57, fig. 2b (only), 1914.

The lectotype of *A. a. globosa* (pl. 4, fig. 21) in the British Museum is marked "x" by me and is a deformed specimen. There is a break in the shell at the second embryonic whorl, which accounts for the depressed spire. The last postembryonic whorl is abnormally rounded and enlarged; postembryonic whorls white lined with cinnamon buff, peripheral band cinnamon buff, subperipheral band white, basal band hazel. On the aperture side of the last whorl, below the periphery, there is another break in the shell which has been repaired by the animal, and the pattern is lacking on approximately 2 mm. of the shell. The shell is thin, sutural band white; the lip is little thickened and colored pale vinaceous drab; the columella callus white. Length 16.4 mm., greater diameter 12.8 mm., spire height 6.5 mm., number of whorls  $5\frac{1}{2}$ .

Specimen A of the type lot (pl. 4, fig. 22) more accurately represents the usual form of *A. a. globosa*. The postembryonic whorls white lined with pinkish buff, last whorl banded with pinkish buff, axially streaked with white, in the umbilical region a band of cinnamon buff, darkening near the edge of the lip to mikado brown. Length 16.8 mm., greater diameter 11.4 mm., number of whorls 6.

Distribution: Nuuanu, Gulick, Baldwin, BBM 11884, J. S. Emerson, BBM 102196; Kalihi, Gulick. Specimens also obtained by Welch in London from Blok and Fulton.

*A. a. globosa* is a distinct subspecies which differs from *vittata* in being a smaller shell, always dextral and having a different range of color patterns. It occurs mixed with *A. a. vittata* in the Gulick collections, and odd specimens identifiable as *globosa* are usually found with typical forms of *vittata* in other collections.

The type lot of *A. a. vittata*, consisting of three specimens, has two specimens which are color patterns of *A. a. globosa*. One of these marked A (pl. 4, fig. 23) is a light color pattern and a narrow form

of the shell. The postembryonic whorls are white lined and banded on the last whorl with hazel, in the umbilical region a patch of carob brown; lip and columella callus vinaceous buff. Length 17.7 mm., greater diameter 11.2 mm., number of whorls  $5\frac{3}{4}$ .

The other specimen B has the usual *A. a. globosa* pattern similar to plate 1, figure 12. The type lot of three shells of *A. a. globosa* has one specimen marked B which is a typical *A. a. vittata*.

The usual form of the shell and color pattern of *A. a. globosa* in the Bishop Museum (pl. 1, fig. 12) has white postembryonic whorls banded and lined with hazel, base entirely hazel. Length 17.4 mm., greater diameter 11.7 mm., spire height 9.0 mm. A specimen from the Gulick collection (pl. 4, fig. 24) has white postembryonic whorls spirally banded with cinnamon buff, which darkens on the last eighth whorl to mikado brown; impressed sutural band cinnamon.

#### ACHATINELLA APEXFULVA HANLEYANA Pfeiffer

PLATE I, FIGURE 16; PLATE 4, FIGURES 25, 26

*Achatinella hanleyana* PFEIFFER, Proc. Zool. Soc. London, 1855, p. 202.

*Achatinella lorata* FÉRUSAC, Pilsbry and Cooke, Man. Conch., vol. 22, pp. 278, 281, 1914.

To quote from Pilsbry and Cooke:

Mr. Sykes remarks that this is "related to the form of *A. lorata* described as *A. nobilis*, and may prove to be an extreme variety." Dr. C. Montague Cooke, on examining the type in the British Museum considered it an artificially colored *lorata*.

The lectotype in the British Museum is not an artificially colored *lorata* but a normal shell which is a distinct subspecies and related to *A. a. globosa*. *A. a. hanleyana* closely resembles *A. a. globosa* in the shape of the bicolored embryonic whorls and in the size and color of the shell. *A. a. hanleyana*, however, is not banded with white but has a solid brown pattern above the periphery. No *A. a. lorata* has bicolored embryonic whorls similar to those of *A. a. globosa*. *A. a. hanleyana*, however, can easily be confused with brown forms of *Partulina radiata* Gould (see Pilsbry and Cooke, 1912-1914, p. 49, pl. 13, fig. 8). The two forms are so close that I have been in doubt as to whether or not to consider *hanleyana* a *Partulina*. However, I am inclined to believe that it is an extinct lowland *Achatinella*, because of its similarity to *A. a. globosa* and to a sinistral *Achatinella* (pl. 4, fig. 26) obtained by Dos Santos in Kalihi Valley, which has embryonic whorls very similar to those of *A. a. hanleyana* (pl. 1, fig. 16). *A. a. hanleyana*, moreover, has an impressed sutural band, a columella cal-



lus, and a rugose texture to the surface of the shell, not usual in specimens of *Partulina* from Oahu. *Partulina radiata* is placed by Pilsbry with *Partulinas* from the Island of Maui. In some collections the shells are labeled Maui. However, *radiata* is typically an Oahu shell and probably comes from the region of Nuuanu Valley.

The lectotype (pl. 4, fig. 25) has the first embryonic whorl colored terra cotta, next whorl upper half cartridge buff, lower half shades from terra cotta to pale vinaceous fawn and finally cartridge buff, remainder of the embryonic whorls cream buff; the first half post-embryonic whorl has the shell nacre worn off, remaining postembryonic whorls pinkish buff, axially streaked with close-set lines of hazel; lip and columella callus cartridge buff. Length 17.8 mm., greater diameter 12.0 mm., number of whorls 6. The surface of the shell does not seem smooth but slightly rugose as compared with *A. a. globosa*, but this rugosity of the surface may be an illusion caused by the axial streaking.

From Arthur Blok I obtained a specimen (pl. 1, fig. 16) which greatly resembles the holotype of *A. a. hanleyana* in form and color pattern. The postembryonic whorls ochraceous buff, axially streaked with tawny, subperipheral band ochraceous buff; the shell has a rugose appearance; impressed sutural band same as ground color of the shell. Length 19.1 mm., greater diameter 12.4 mm., spire height 9.9 mm.

In the Thurston collection a sinistral shell (pl. 4, fig. 26) collected by Dos Santos and reported from Kalihi has a ground color that matches that of *A. a. hanleyana*. The main difference is that the shell is heavily banded with dark bands. The postembryonic whorls are warm buff axially streaked with ochraceous tawny and banded with liver brown; lip and columella callus pale vinaceous fawn. This shell closely resembles the form of *A. a. simulans* var. 1 on the Kamanaike-Kalihi Ridge. Probably it came from somewhere in the Kalihi region at a similar elevation, possibly on the north side of the valley. This sinistral shell may come from a colony of pure sinistral *hanleyana* of which this is the dark color form. The dextral race is probably from a colony of still lower elevation occurring directly below the sinistrals.

ACHATINELLA APEXFULVA HANLEYANA var. 1

PLATE I, FIGURE 17; PLATE 4, FIGURE 32

A peculiar form of *Achatinella apexfulva* was procured from Sowerby and Fulton in London. The shells were accompanied by no

data concerning their locality, but the fact that they have pointed *globosa*-like embryonic whorls leads me to believe that they are a lowland form of *hanleyana* which comes from somewhere in the general region of Nuuanu to Kalihi. However, I may be wrong in this belief and the shells may be lowland forms of *Partulina radiata* Gould. The first embryonic whorl (pl. 1, fig. 17) is fawn color, next whorl pale pinkish cinnamon, shading to pinkish buff; postembryonic whorls pinkish buff, axially streaked with mikado brown and spirally lined on the last whorl above the periphery with pinkish buff; impressed sutural band the ground color; columella callus white; lip tilleul buff. Length 20.8 mm., greater diameter 12.5 mm., spire height 10.8 mm., number of whorls 6½.

The shell may have a darker pattern (pl. 4, fig. 32). Postembryonic whorls clay color, axially streaked with mikado brown, spirally lined with cinnamon buff, last whorl below the periphery with a band of white, about the base a band of cream color; lip outer edge pinkish buff; columella callus and inner edge of lip white. Length 19.9 mm., greater diameter 12.6 mm., spire height 9.8 mm.

#### ACHATINELLA APEXFULVA SIMULANS Reeve

PLATE 1, FIGURE 19; PLATE 4, FIGURES 33-35a

*Achatinella simulans* REEVE, Conch. Icon., vol. 6, pl. 2, fig. 15, April 1850.

*Achatinella vittata simulans* REEVE, Pilsbry and Cooke, Man. Conch., vol. 22, p. 292, pl. 57, fig. 8 (figs. 9-11, 14a, pl. 57, not *A. simulans* of Reeve 1850, but *A. a. rubidipicta*, new subspecies), 1914.

The shell is a small lowland form, with a dark brownish band in the umbilical region, one at or just below the edge of the periphery, one just below the periphery; above the periphery on the last whorl just behind the edge of the lip a patch of brown or group of brown lines.

The type lot of *A. a. simulans* contains three specimens none of which agree with Reeve's original figure (pl. 4, fig. 33). One specimen (pl. 4, fig. 34) in the type lot approaches the color pattern of the original figure and is considered the lectotype. It differs from the original figure in having a flat columella callus and in not having a subsutural band on the last two whorls and three dark chocolate sub-peripheral bands. The embryonic whorls are bicolored similar to those of *A. a. globosa*, first embryonic whorl deep mouse gray, later embryonic whorls white; postembryonic whorls white with a band of cinnamon just above or at the edge of the periphery, above the periphery on the last whorl just behind the edge of the lip a streak or patch of mikado brown, below the edge of the periphery a band of



warm sepia about the base, surface rough and pitted; impressed sutural band white; lip and columella callus cartridge buff. Length 18.5 mm., greater diameter 13.2 mm., number of whorls  $5\frac{3}{4}$ .

Distribution, area 16: **Kamanaiki-Kalihi Ridge**, locality 121-2, elevation 1,300-1,350 feet, H. Lemke and H. Lemke, Jr., 1934, BBM 114979, HL 128 (figs. 3, 3a, p. 29); **Kalihi**, Gulick, BBM 70464, Wilder, BBM 50544. Lectotype specimen "x" type lot BM marked by me.

Until shells were found in area 16, the only region containing shells similar to *A. a. simulans* was that of area 11. However, no white specimen in area 11 is found having a dark band about the umbilicus plus dark bands on the last whorl similar in arrangement to those on either the lectotype or the original figure. What Reeve called *A. decora* closely matches a color pattern of *A. a. rubidipicta* (area 11).

Plate 1, figure 19, shows the usual form of the shell in the Lemke lot from area 16, and a color pattern close to that of figure 34; the postembryonic whorls white, last whorl just below the impressed sutural band and below the periphery lined with cinnamon, basal band in the umbilical region sayal brown. Length 18.0 mm., greater diameter 11.7 mm., spire height 9.4 mm., number of whorls  $6\frac{1}{4}$ .

An obese specimen (pl. 4, fig. 35) looks more like the form of figure 34; the postembryonic whorls white, banded on the first postembryonic whorl with cinnamon, on the penultimate and last whorl lined with chocolate, last whorl below the periphery with a line of chocolate, two lines of clay color, a line of chocolate, and a band of chocolate in the umbilical region. Length 18.7 mm., greater diameter 12.3 mm., spire height 9.6 mm. One specimen (pl. 4, fig. 35a) has the last two whorls colored pale pinkish buff streaked with cinnamon buff and clay color and spirally lined with verona brown and warm sepia.

The color patterns of figures 35 and 35a indicate that yellow forms may occur at higher elevations. Quite possibly *A. a. simulans* is an intermediate race between a form of *A. a. albofasciata* and the lower form of *A. a. simulans* var. 1.

#### ACHATINELLA APEXFULVA SIMULANS var. 1

PLATE 1, FIGURE 20; PLATE 4, FIGURES 36, 36a

Area 17: **Kamanaiki-Kalihi Ridge**, locality 121, elevation 1,300-1,350 feet, Lemke and Lemke, Jr., 1934, BBM 114976, HL 127; 121-1, elevation 1,300 feet, Anderson and Kondo, 6 sinistral 1935 (figs. 3, 3a, p. 29).

The color patterns of area 17 tend to be darker than those of *A. a. simulans*, although individual shells in both areas 16 and 17 may have very similar patterns. A shell with the usual form and color pattern of the shell (pl. 1, fig. 20) has the postembryonic whorls white, banded with warm blackish brown, last whorl lined and tinted above the periphery with cinnamon buff, and a line of cinnamon buff on the white subperipheral band, about the umbilicus a band of cream color; lip and columella callus white, tinted with pale vinaceous fawn. Length 17.6 mm., greater diameter 12.0 mm., spire height 9.1 mm., number of whorls  $6\frac{1}{2}$ .

Another specimen (pl. 4, fig. 36) has the usual form and a light color pattern of the shell; postembryonic whorls white, lined with cinnamon buff and cinnamon; impressed sutural band white, on the penultimate whorl, just above the suture of the whorl below, a line of warm sepia, last whorl lined at the edge of the periphery with warm sepia, base banded with carob brown and a band of black in the umbilical region; lip and columella callus white, streaked with pale brownish vinaceous. Length 17.7 mm., greater diameter 12.3 mm., spire height 9.0 mm. This specimen of figure 36 resembles Reeve's original figure of *A. a. simulans*. The darkest color pattern (pl. 4, fig. 36a) is a warm blackish brown on the postembryonic whorls, last whorl banded at the periphery with a band of white which is lined with two lines of mikado brown, below the periphery a line of cinnamon buff; impressed sutural band sayal brown shading to pale pinkish buff at the upper edge.

#### ACHATINELLA APEXFULVA SIMULANS var. 2

PLATE I, FIGURE 23; PLATE 5, FIGURES 5-5b

Area 19: **Manaiki-Moanalua Ridge**, locality 151B\*, elevation 1,400-2,150 feet, Meinecke, 1932, also collected by O. H. Emerson, BBM 103963, A. MacAuley, in J. S. Emerson collection, BBM 102208, Thurston, BBM 131112.

Area 19A: **Moanalua Stream**, locality 150B-2, elevation 900 feet, Welch and W. Giffard, 1935 (figs. 4, 4a, p. 53).

The usual form of the shell (pl. 1, fig. 23) in area 19 has the postembryonic whorls white, lined with tawny, with a patch of close-set ochraceous tawny lines on the first half postembryonic whorl; impressed sutural band tawny; peripheral and basal bands mars brown or chocolate, with the bands in the umbilical region seal brown or black; lip and columella callus light vinaceous fawn. Length 18.5 mm., greater diameter 12.3 mm., spire height 9.9 mm., number of whorls  $6\frac{1}{4}$ .

The shell may lack the dark chocolate bands (pl. 5, fig. 5) and have the last two postembryonic whorls white, lined with pinkish buff above the periphery, at and below the periphery with sayal brown, base tinted with cream color. The postembryonic whorls may be almost entirely white (pl. 5, fig. 5a) except for a patch of sayal brown on the impressed sutural band on the first and fourth postembryonic whorl, and a band and a line of ochraceous tawny on the base. A yellowish pattern (pl. 5, fig. 5b) is very much like the yellowish pattern of *A. a. simulans* (pl. 4, fig. 35a), and also that of *A. a. rubidipicta* (pl. 5, fig. 2d), postembryonic whorls pinkish buff, lined and banded with ochraceous tawny and tawny, about the periphery and below the ground is white, banded below the periphery with russet deepening to chocolate on the last half whorl.

This race has been considered a variety of *A. a. simulans* because of its small size and similarity in form. In a fossil bed, locality 150B-2, a few specimens of *apexfulva* are found and may be considered the extreme limit of this race of *simulans* var. 2, although it is probable that, were there more specimens obtainable retaining a sufficient amount of the color pattern, it might prove to be another variety.

#### GROUP OF *A. A. VITTATA* REEVE

##### **ACHATINELLA APEXFULVA VITTATA** Reeve

PLATE I, FIGURE 13; PLATE 4, FIGURES 17-20b

*Achatinella vittata* REEVE, Conch. Icon., vol. 6, pl. 2, fig. 9, April 1850.—PILSBRY and COOKE, Man. Conch., vol. 22, p. 289, pl. 57, figs. 1, 2, 2a, 2c (only), 1914.

The holotype of *A. a. vittata* in the British Museum has a spot of red sealing wax on the aperture side of the shell (pl. 4, fig. 17). Postembryonic whorls white, penultimate banded with avellaneous, last whorl above the periphery with two bands of avellaneous and a subperipheral band of pinkish buff, below the periphery banded and lined with fawn color, and a band of army brown in the umbilical region; lip and columella callus pale vinaceous fawn. Length 19.0 mm., greater diameter 12.7 mm., spire height 10.0 mm., number of whorls 6.

Distribution, area 12: **Nuuanu**, Gulick; **Hillerbrand's Glen**, **Nuuanu**, locality 100E-1\*, elevation 1,000-1,500 feet, R. A. Cooke, BBM 58284, and C. M. Cooke, BBM 22119, 19916 (figs. 3, 3a, p. 29). Dr. C. M. Cooke tells me that these shells come from somewhere along the ridge on which locality 100E-1\* is plotted. They were probably collected on the lower portion of the ridge at an elevation of around 1,000-1,500 feet, because Meinecke reports the larger race of *A. a.*

*rubidipicta* near the head of this subridge on the Nuuanu-Kapalama Ridge. Further collecting will establish the exact location of this race.

The specimens of *A. a. vittata* from Nuuanu collected by Gulick closely match the holotype. The shells may be dextral or sinistral. A sinistral specimen (pl. 1, fig. 13), is very similar to the color pattern of the type; postembryonic whorls white, lined and streaked with cinnamon buff or pinkish buff and lined with mikado brown. A darker color pattern (pl. 4, fig. 18) has the penultimate whorl banded with pinkish buff shading to avellaneous and fawn color on the last whorl; impressed sutural band and subsutural band pale pinkish buff.

The R. A. Cooke and C. M. Cooke, Jr., lots are not typical *vittata* but contain patterns similar to those of typical *vittata*. The locality is a wide one and probably represents a mixture of typical *vittata* with typical *rubidipicta* patterns. In the C. M. Cooke lot, which may represent a collection of shells taken mostly from the lower portion of locality 100E-1\*, 36 percent of the shells have a pattern similar to that of plate 4, figure 19, penultimate whorl light buff banded with white, the last whorl banded with white below the subsutural band of light buff, at and below the periphery banded and lined with ochraceous tawny and tawny axially streaked with light buff, base banded with white, and lined and banded with mars brown. A rare brown pattern (pl. 4, fig. 19a) has the last whorl and a half colored light buff below the suture, just above and below the periphery the ground is axially streaked and banded and tinted with tawny and russet.

In the R. A. Cooke lot color patterns are closer to *A. a. rubidipicta* and probably come from a region adjacent to area 11. The typical form and color pattern of the shell in the R. A. Cooke lots (pl. 4, fig. 20) has the penultimate whorl white, lined with cinnamon buff, impressed sutural band cinnamon, last whorl above the periphery pale pinkish buff lined with pinkish buff and verona brown, edge of the periphery banded with vandyke brown and a band of white, sub-peripheral band vandyke brown, remainder of the base white, sutural band pinkish cinnamon. Length 18.7 mm., greater diameter 13.0 mm., spire height 9.5 mm. The shell may have an entirely white ground (pl. 4, fig. 20a), the last whorl profusely lined with walnut brown and chocolate; impressed sutural and subsutural bands light buff. A dark color pattern (pl. 4, fig. 20b) has the penultimate whorl warm buff, banded and streaked with ochraceous tawny on the upper

half of the whorl, including the impressed sutural band, lower half mars brown, last whorl the impressed sutural and subsutural bands ochraceous tawny, remainder of the whorl carob brown, lined with white.

**ACHATINELLA APEXFULVA VITTATA var. 1**

PLATE 1, FIGURE 9; PLATE 4, FIGURES 15-15b

*Achatinella vittata* REEVE, Pilsbry and Cooke, Man. Conch., vol. 22, p. 290, pl. 57, figs. 3-3b (only), 1914.

Area 8: **Pauoa-Nuuanu Ridge**, locality 91A\*, elevation 1,500-1,800 feet, Meinecke, 1923, 1925, 1926, 4 sinistral 1931. Also locality 90A\*, elevation 1,400-1,450 feet, Meinecke, 1922; 90A-1\*, elevation 1,400 feet, Lemke, 1932; 93A\*, elevation 1,500-1,800 feet, 7 sinistral 1928; 94A\*, elevation 1,700 feet, 1927, 1928, 1931; 95A\*, elevation 1,750 feet, Meinecke, 1927, 1931 (figs. 3, 3a, p. 29). Other collectors are J. S. Emerson, BBM 102189, E. D. Baldwin, BBM 56644-56646, Wilder, BBM 50498, Thurston shells collected by Dos Santos, BBM 131084, A. F. Judd, BBM 110294-110299.

The usual form of the shell is darker than *A. a. vittata*, both in the shade of yellow on the early postembryonic whorls and in the reddish-brown banding on the last whorl. Large series of shells of *A. a. vittata* and *A. a. vittata* var. 1 are separable, but individual specimens from each race are indistinguishable. The usual form of *vittata* var. 1 (pl. 1, fig. 9) has the first half postembryonic whorl white axially streaked with cinnamon buff, penultimate whorl white axially streaked with cinnamon buff, spirally banded with dark vinaceous brown and white, last whorl banded and lined with white and dark vinaceous drab, below the periphery lines of dark vinaceous brown; impressed sutural band shades from tawny, on the first whorl, to cinnamon on the last; subsutural band on the last whorl also cinnamon; lip and columella callus vinaceous fawn. Length 18.8 mm., greater diameter 12.5 mm., spire height 9.5 mm., number of whorls 6.

An elongate specimen (pl. 4, fig. 15) measures: Length 18.6 mm., greater diameter 11.6 mm., spire height 10.5 mm.; first postembryonic whorl and penultimate whorl, white faintly tinted and axially streaked with pinkish buff and lined with cinnamon, last whorl above the periphery white, lined and streaked with pinkish buff, and a band of snuff brown above the periphery, peripheral band white with a line of chocolate at the upper margin of the band, below the periphery banded and lined with dark vinaceous brown; impressed sutural band changes from tawny to cream buff.



An obese shell (pl. 4, fig. 15a) shows the lightest color form of this race; postembryonic whorls white spirally lined with pinkish buff, below the periphery of the last whorl a faint line of verona brown, below which are faint bands of pinkish buff, on the last fourth whorl the bands are darker above and below the periphery, being warm sepia and mikado brown. Length 17.3 mm., greater diameter 12.7 mm., spire height 8.9 mm. The darkest color pattern (pl. 4, fig. 15b) has the postembryonic whorls light ochraceous buff, banded and axially streaked with hay's brown and sorghum brown, base lined with white. The color patterns of figures 15a and 15b are rare patterns occurring only on a few specimens in area 8.

**ACHATINELLA APEXFULVA VITTATA var. 2**

PLATE 1, FIGURE 10; PLATE 4, FIGURES 16, 16a

*Achatinella vittata* REEVE, Pilsbry and Cooke, Man. Conch., vol. 22, p. 290, pl. 57, figs. 4, 4a, 5-5b (only), 1914.

Area 9: **Glen Ada, Nuuanu**, locality 100-2\*, approximate elevation 1,200-1,500 feet, R. A. Cooke, C. M. Cooke (figs. 3, 3a, p. 29).

While series of shells from area 9 are quite distinct from typical *A. a. vittata* or *A. a. vittata* var. 1, because of the dominance of light color patterns, nevertheless the color patterns of area 9 are repeated in other areas and mixed lots are difficult to separate.

The usual form of the shell (pl. 1, fig. 10) has white postembryonic whorls, banded on the last half of the penultimate with two bands of fawn color, last whorl above the periphery banded with two bands of cameo brown, lined below the suture with cinnamon buff, the lines being broken with axial streaks of white, subperipheral band cameo brown; sutural band cinnamon buff; lip and columella callus vinaceous buff. Length 18.9 mm., greater diameter 12.3 mm., spire height 9.9 mm., number of whorls 6.

The lightest color pattern (pl. 4, fig. 16) has white postembryonic whorls lined on the last whorl with walnut brown. An obese shell and a rare dark color pattern (pl. 4, fig. 16a), found on only 6 percent of the shells in the R. A. Cooke lot, has the postembryonic whorls white, last whorl above the periphery banded with pinkish buff axially streaked with cinnamon, banded at and below the periphery with chocolate; impressed sutural band shades from tawny to ochraceous tawny. Length 18.5 mm., greater diameter 12.8 mm., spire height 9.7 mm.

## ACHATINELLA APEXFULVA CINEREA Sykes

PLATE 1, FIGURE 11; PLATE 4, FIGURE 37; PLATE 5, FIGURES 1, 1a

*Achatinella vittata* var. *cinerea* SYKES, Fauna Hawaiiensis, p. 305, 1900.*Achatinella vittata cinerea* SYKES, Pilsbry and Cooke, Man. Conch., vol. 22, pp. 289, 291, pl. 57, figs. 6-7, 1914.

The holotype (pl. 4, fig. 37) has the first postembryonic whorl buckthorn brown, penultimate whorl banded with avellaneous, white, and dark olive buff, last whorl ground white banded with maroon or hay's maroon; impressed sutural band and subsutural band white; columella callus vinaceous fawn; lip vinaceous fawn banded with white. Length 18.7 mm., greater diameter 12.4 mm., number of whorls  $6\frac{1}{2}$ .

Distribution, area 10: Nuuanu, locality 100B-7?, elevation 1,250-1,400 feet, Meinecke, 1911, 1914, 1916; 100B-12, elevation 1,150-1,250 feet; 100B-13, elevation 1,150-1,350 feet; 100B-14, elevation 1,250-1,500 feet, 1 sinistral, all collected by C. M. Cooke, Jr. (figs. 3, 3a, p. 29). The Meinecke locality may be wrongly plotted one ridge south of where it actually is, because Dr. Cooke, who carefully worked over this section of Nuuanu and made sketch maps of the region, does not report any *apexfulva* from the region of locality 100B-7? Other collectors of *A. a. cinerea* are Wilder, BBM 50504, R. A. Cooke, BBM 58138. Holotype in BM, collected in Nuuanu by Perkins.

The usual color pattern and form of the shell (pl. 1, fig. 11) has the first embryonic whorl warm sepia, next whorl upper fourth pale pinkish buff, remainder of the whorl shades from prout's brown to buckthorn brown, last embryonic whorl upper fourth white, lower three-fourths warm buff finely lined with white; first postembryonic whorl and first half of penultimate banded with a light shade of buckthorn brown and warm buff, last half of penultimate, and first half of last whorl above the periphery, drab gray, banded below the white sutural band, with a band of wood brown shading to chocolate, a band of white, and 2 bands of chocolate, last half of the last whorl chocolate, banded and lined with white, below the periphery last whorl white, banded with chocolate, in the umbilical region a patch of naples yellow, banded with chocolate. Length 19.1 mm., greater diameter 13.1 mm., spire height 9.3 mm., number of whorls 6.

The color pattern may be light gray (pl. 5, fig. 1); first postembryonic whorl and first half of the penultimate white faintly tinted with pinkish buff, last whorl and a half shades from pale smoke gray to smoke gray on the last whorl, banded, lined, and finely axially streaked with white—the last half whorl is also lined above



the periphery with fawn color—below the periphery banded with a band of warm sepia lined with smoke gray, the aperture side of the last whorl has a line of warm sepia above the white basal band. An elongate specimen (pl. 5, fig. 1a), length 19.8 mm., greater diameter 12.8 mm., spire height 10.0 mm., shows the darkest color form, the last whorl banded with white and chocolate.

#### ACHATINELLA APEXFULVA ALBOFASCIATA Smith

PLATE I, FIGURE 14; PLATE 4, FIGURES 27-28b

*Apex albofasciatus* SMITH, Proc. Zool. Soc. London, 1873, p. 78, pl. 9, fig. 21.  
*Achatinella vittata simulans* REEVE, Pilsbry and Cooke, Man. Conch., vol. 22, pp. 292, 293, pl. 57, figs. 12, 13, 14a, 14c (only), 1914.

The holotype of *A. a. albofasciata* (pl. 4, fig. 27) in the British Museum is marked with a red dot of sealing wax. The postembryonic whorls are cinnamon buff darkening to sayal brown on the last half whorl, banded on the last whorl at the edge of the periphery with white and in the umbilical region with white and light pinkish cinnamon; impressed sutural band white; lip and columella callus pale pinkish buff. Length 18.5 mm., greater diameter 12.6, spire height 9.0 mm., number of whorls  $5\frac{3}{4}$ .

Distribution, area 13?: **Kapalama Stream**, locality 110A-1?, "N. Bank opposite Waiolani Peak. Halfway from top to bottom of Gulch, elevation 1,500-1,550, Herb. Alani [*Pelea*]," L. A. Thurston 1911, BBM 131103-131106 (figs. 3, 3a, p. 29). Also collected in **Kapalama** by W. D. Wilder, BBM 50543, D. Fraser, BBM 15838, and Dos Santos for Thurston, BBM 131095-131096.

The Thurston lots contain 37 dextrals and 4 sinistrals. The usual form of a dextral (pl. 1, fig. 14) has the last half of the first postembryonic whorl, and the first half of the penultimate whorl, pinkish buff axially streaked with cinnamon buff, last half of the penultimate pale pinkish buff banded with light pinkish buff, shading on the last whorl to pinkish buff finely lined and streaked with white or pale pinkish buff, at the edge of the periphery a wide band of white; impressed sutural band pinkish buff; lip light vinaceous fawn spotted with white. Length 19.8 mm., greater diameter 12.3 mm., spire height 10.8 mm., number of whorls  $6\frac{1}{2}$ . A sinistral specimen (pl. 4, fig. 28b) is very like the holotype, differing in being banded with white above the periphery and about the base, last two whorls with bands of cinnamon buff streaked with cinnamon. The Kapalama form of *A. a. albofasciata* is very close in form to *A. a. rubidipicta*. From Thurston's description it occupies an area just below *A. a. rubidipicta* (area 11). A few specimens of *A. a. albofasciata* are often found in lots

of *A. a. rubidipicta*, and probably come from the border region between areas 11 and 13.

The darkest color form of the shell is shown in plate 4, figure 28, the last two whorls are tawny axially streaked and lined with ochraceous buff, on the last whorl a wide band of white at the periphery. The lightest color pattern (pl. 4, fig. 28a) is entirely white on the last two whorls lined with ochraceous tawny.

**ACHATINELLA APEXFULVA ALBOFASCIATA var. 1**

PLATE 1, FIGURE 21; PLATE 4, FIGURES 29, 29a

Distribution, area 14??: Kalihi, J. S. Emerson collection, BBM 102205-102207, collected by Gomes and W. B. Olson. The exact position of the locality is unknown, but has been plotted by me on the Kamaikai-Kalihi Ridge opposite area 13? (fig. 3a, p. 29), because of the similarity of this form to *A. a. albofasciata*. This form should be collected again and the exact locality determined.

The shells have a lighter color pattern than *A. a. albofasciata*. The shade of the color pattern of the Kalihi shells best matches the holotype of *A. a. albofasciata*, but the banding of the Kapalama shells is closer to that of the holotype of *albofasciata* and for this reason Kapalama is considered the region of the type locality. The Kalihi shells are dominantly sinistral and composed of light color patterns. Forms similar to plate 4, figure 28, are not found in this Kalihi lot. Out of 34 shells, 9 are dextrals.

The typical form of the shell (pl. 1, fig. 21) is smaller than the usual form of *albofasciata* from Kapalama, the postembryonic whorls cinnamon buff faintly lined and streaked with white; impressed sutural band the color of the ground; last whorl below the edge of the periphery white, lined with cinnamon buff; lip and columella callus pale cinnamon pink. Length 18.1 mm., greater diameter 12.3 mm., spire height 9.7 mm., number of whorls 6.

The lightest color pattern (pl. 4, fig. 29) has the postembryonic whorls white, lined with cinnamon buff. The dextral form of the shell (pl. 4, fig. 29a) has the last two whorls light buff, axially streaked and lined with ochraceous buff, last whorl at the periphery and below the periphery banded with white. This form looks very much like yellow forms of *A. a. globosa* (pl. 4, fig. 24).

**ACHATINELLA APEXFULVA OLIVERI, new subspecies**

PLATE 1, FIGURE 18; PLATE 4, FIGURES 30-31

This form is intermediate between the more globose upper race of *A. a. albofasciata* and the smaller form of *A. a. simulans* var. 1.

The first postembryonic whorl of the holotype (pl. 1, fig. 18) is pale pinkish cinnamon spirally lined, banded, and tinted with sayal brown, last two whorls sayal brown, last whorl below the periphery banded and lined with white; impressed sutural band white; lip and columella callus light vinaceous fawn. Length 19.7 mm., greater diameter 12.5 mm., spire height 11.0 mm., number of whorls 6 $\frac{3}{4}$ .

Distribution, area 15?: **Kamanaiki Stream**, type locality 120-1?, O. H. Emerson, BBM 103962; also collected by J. S. Emerson, BBM 102203-102204, Dos Santos, BBM 74301, and Thwing, BBM 28544-28546 (figs. 3, 3a, p. 29). The locality has not been found in recent years. Only an approximation has been made by Dr. C. M. Cooke, and Dr. Oliver Emerson which is somewhere in the vicinity of the locality. The shell is named after Dr. Oliver Emerson, who discovered it.

A dark white-lined color pattern (pl. 4, fig. 31) has the last two whorls banded with russet and lined with white. The darkest color pattern (pl. 4, fig. 30) has the last two whorls liver brown axially streaked with hazel, about the periphery of the last whorl a line of white; impressed sutural band white. The lightest color pattern (pl. 4, fig. 30a) is white, lined on the last two whorls with hazel. This pattern occurs on only one shell in the type lot.

**ACHATINELLA APEXFULVA RUBIDIPICTA, new subspecies**

PLATE I, FIGURE 15; PLATE 5, FIGURES 2-2d

*Achatinella vittata simulans* REEVE, Pilsbry and Cooke, Man. Conch., vol. 22, p. 292, pl. 57, figs. 9-11, 14b (only), 1914 (not of Reeve 1850).

The shell is larger than *A. a. simulans*, having a characteristic smooth surface, and usually having spiral bands which are generally not broken by axial streaks. The form is closest to that of *A. a. cinerea*, having an inflated last whorl. The holotype (pl. 1, fig. 15) has the first half of the first embryonic whorl rood's brown, last half upper portion white, the lower half rood's brown changing to mouse gray on the next whorl, on the last half of the second embryonic whorl and on the remaining embryonic whorls the lower band is a faint shade of cream buff, upper band white; the postembryonic whorls white, the first half of the first postembryonic whorl banded on the lower fourth of the whorl with cinnamon buff, penultimate and last whorls lined with cinnamon, last half of penultimate and last whorl banded at the edge of the periphery with burnt umber, last whorl below the periphery with a line of burnt umber; lip and

columella callus pale vinaceous fawn. Length 19.5 mm., greater diameter 13.2 mm., spire height 10.2 mm., number of whorls 6 $\frac{3}{4}$ .

Distribution, area 11: **Nuuanu-Kapalama Ridge**, type locality 110\*, elevation 1,750-1,870 feet, Meinecke, 1921, 1922, 1927, 1929; also locality 111\*, elevation 1,800-2,100 feet, Meinecke, 1 sinistral 1929 (figs. 3, 3a, p. 29).

The color pattern of 11 percent of the shells (pl. 5, fig. 2) is a more heavily lined one; the last two whorls may be white, lined and banded on the penultimate with mikado brown, on the last whorl banded with vandyke brown and lined with mikado brown, base banded with seal brown, umbilical region tinted with cream buff. Twenty-four percent are conspicuously banded; last two whorls white, (pl. 5, fig. 2a) banded with chocolate and lined on the penultimate with a subsutural band of mikado brown, which splits into two lines on the last half of the penultimate and fades out on the last half of the last whorl. The darkest color pattern and elongate form of the shell (pl. 5, fig. 2b), occurring on 2 percent of the shells, has the last two whorls burnt umber axially streaked with cinnamon and banded on the last whorl with white; impressed sutural band chocolate shading to cinnamon buff at the upper edge. Length 19.8 mm., greater diameter 12.8 mm., spire height 9.9 mm. This shell resembles the dark color pattern of *A. a. cinerea* (pl. 5, fig. 1a). The main difference is that *A. a. cinerea* has the embryonic whorls banded with yellow and the first two postembryonic whorls banded with yellow and gray. The obese form and lightest color pattern of the shell (pl. 5, fig. 2c) measures: Length 19.0 mm., greater diameter 13.8 mm., spire height 9.4 mm.; postembryonic whorls white, below the impressed sutural band a line of cinnamon deepening to warm sepia on the last whorl, the base lined and banded with chocolate. This white color pattern occurs on 20 percent of the shells. Eight percent have a yellow color pattern which looks like an intermediate form between *rubidipicta* and *albofasciata*. One of these (pl. 5, fig. 2d) has the last whorl and a half pale pinkish buff axially streaked and lined with cinnamon, banded with white at the edge of the periphery, below the periphery banded with amber brown, and a basal band of pinkish buff; impressed sutural band pinkish buff axially streaked with cinnamon. In some collections specimens of *A. a. albofasciata* are found mixed with lots of *A. a. rubidipicta*. The reason for this is that the shells were either collected in a locality intermediate between areas 11 and 13 or all the shells from areas 11 and 13 were lumped together in one locality.

**ACHATINELLA APEXFULVA RUBIDIPICTA var. 1**

PLATE 5, FIGURES 3-3b

Area?: **Kalihi**, Wilder, BBM 50544, 9 dextral, 16 sinistral.

The shells are similar to *A. a. rubidipicta* but have a different series of color patterns. Some dextral specimens have a color pattern which resembles *A. a. albofasciata* and differs only in having light reddish-brown bands instead of yellowish-brown ones. One of these distinctive color patterns (pl. 5, fig. 3) is a white shell banded and lined on the last two whorls with pecan brown, and a band of ochraceous tawny below the periphery. The usual form of a dextral shell (pl. 5, fig. 3a) measures: Length 19.7 mm., greater diameter 13.0 mm., spire height 10.0 mm.; last two postembryonic whorls white, with a band of russet below the white sutural band and just above the edge of the periphery, last whorl lined at the edge of the periphery with two lines of burnt umber, below the periphery lined and banded with burnt umber on the rest of the whorl. The sinistral form of the shell (pl. 5, fig. 3b) is very like typical *A. a. rubidipicta* but the distribution of the chocolate bands over the white ground on the last two whorls is different from anything found in locality 110.

**ACHATINELLA APEXFULVA RUBIDIPICTA var. 2**

PLATE 1, FIGURE 22

Area 18: **Kalihi-Kahauiki Ridge**, locality 141\*, elevation 1,650 feet, Meinecke, 2 sinistrals 1927 (figs. 3, 3a, p. 29). Also collected in **Kahauiki** by Wilder, BBM 50519. The usual color pattern of the shells in the Wilder lot is similar to that of the two Meinecke shells, and they are believed to have come from the same locality.

The form is very close to *A. a. rubidipicta* but has a slightly different series of color patterns. The usual color pattern (pl. 1, fig. 22) has the last two postembryonic whorls white, lined below the suture with a line of mikado brown, last whorl banded with two chocolate bands. Length 19.8 mm., greater diameter 13.4 mm., spire height 10.2 mm. The color pattern may be lined similar to plate 5, figure 3b.

**ACHATINELLA APEXFULVA RUBIDIPICTA var. 3**

PLATE 5, FIGURES 4-4e

Area?: **Moanalua**, Wilder, BBM 50522.

The subspecies resembles *A. a. rubidipicta* but has a different series of color patterns. The embryonic whorls are similar to those of *A. a. simulans* var. 2, and are intermediate in form and color



pattern between *A. a. ozum* and *A. a. rubidipicta*. The shells probably came from above area 19 on the Manaiki-Moanalua Ridge.

The usual form of the shell and the color pattern of 52 percent of the specimens (pl. 5, fig. 4) has the postembryonic whorls white, lined with cinnamon and mikado brown, and banded with chocolate, last whorl subperipheral band white, below which is a line of cinnamon and cinnamon buff, base chocolate; impressed sutural band cinnamon; lip and columella callus light vinaceous fawn. Length 19.6 mm., greater diameter 13.0 mm., spire height 9.8 mm., number of whorls  $6\frac{1}{2}$ .

An elongate shell (pl. 5, fig. 4a) measures: Length 19.3 mm., greater diameter 12.5 mm., spire height 9.5 mm.; last two postembryonic whorls pale pinkish buff, profusely lined and banded with russet and mars brown, impressed sutural band cinnamon. An obese form of the shell (pl. 5, fig. 4b) with light color pattern found on 31 percent of the shells has the postembryonic whorls white, lined with pinkish buff; impressed sutural band pinkish buff; last whorl banded at the edge of the periphery with a band and below the periphery with bands and lines of chocolate. Length 19.1 mm., greater diameter 13.4 mm., spire height 9.1 mm.

Seven percent have a lined spiral pattern (pl. 5, fig. 4c); postembryonic whorls above the periphery lined with russet, peripheral band narrow, about 0.5 mm. instead of nearly 2 mm. as in figure 4, banded below and at the periphery with chocolate. The darkest pattern (pl. 5, fig. 4d) on 9 percent, is russet, streaked with cinnamon buff on the first half of the penultimate, last half of penultimate ochraceous tawny axially streaked with burnt umber, last whorl chocolate, axially streaked with ochraceous tawny. A single specimen (pl. 5, fig. 4e) has a white ground lined with warm buff; impressed sutural band ochraceous tawny fading to white on the last whorl. This pattern is very similar to lined patterns of *A. a. albofasciata*.

#### GROUP OF *A. A. PILSBRYI* NEW SUBSPECIES

##### **ACHATINELLA APEXFULVA PILSBRYI, new subspecies**

PLATE I, FIGURE 29; PLATE 5, FIGURE 27

The holotype (pl. 1, fig. 29) is small, embryonic whorls white; spire pointed, postembryonic whorls white; impressed sutural band tawny; last whorl below and at the periphery banded with tawny and a basal band of kaiser brown; lip fawn color, tuberculate; columella callus white. Length 17.6 mm., greater diameter 12.4 mm., spire height 9.2 mm., number of whorls  $6\frac{1}{2}$ .

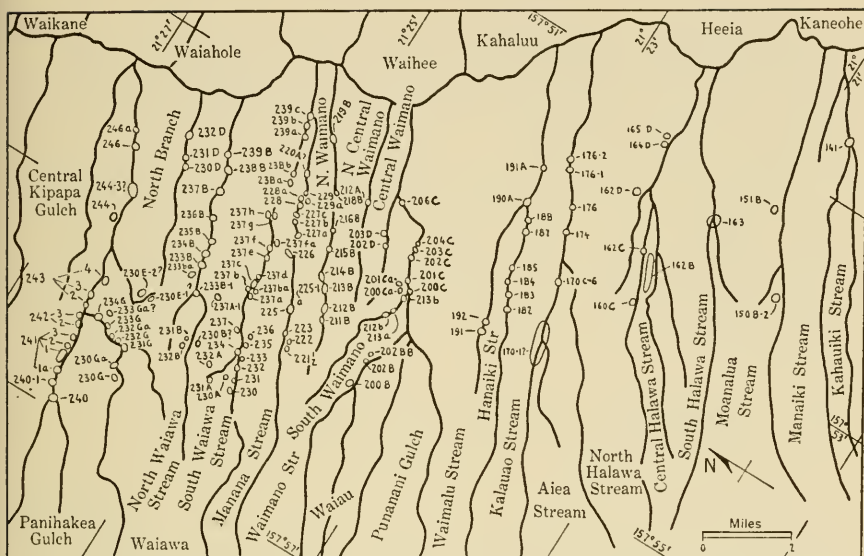


FIG. 4.—Southeast-central Oahu, leeward slope of the Koolau Range, including regions Ia, II, IIIa, half of region III, and two valleys of region I (fig. 7, p. 194), showing localities of subspecies of *A. apexfulva* belonging to the groups of *A. a. cestus*, *A. a. vittata*, *A. a. pilsbryi*, *A. a. turgida*, *A. a. polymorpha*, and *A. a. irwini*.

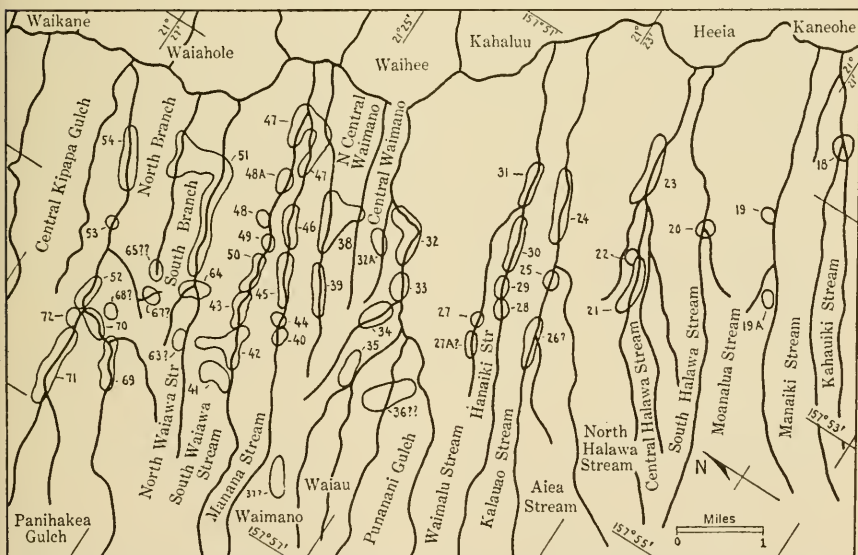


FIG. 4a.—Same as fig. 4, but showing the area occupied by different subspecies of *A. a. apexfulva* belonging to the groups of *A. a. cestus*, *A. a. vittata*, *A. a. pilsbryi*, *A. a. turgida*, *A. a. polymorpha*, and *A. a. irwini*.



Distribution probably somewhere in the region of area 26?: **Aiea-Kalauao Ridge**, approximate locality 170-1?, Judd, BBM 110210, and Cooke, BBM 72494 (figs. 4, 4a, p. 53). The subspecies is named after Dr. Henry A. Pilsbry. The shell has not been found in many years and may be extinct.

The form of a broadly banded juvenile shell (pl. 5, fig. 27) has an elongate spire. Length 16.9 mm., greater diameter 11.6 mm., spire height 9.0 mm. Postembryonic whorls white, banded with cinnamon, last whorl below the periphery cinnamon, lined with two lines of white and a line of mikado brown. The shell is a dead specimen and the color has faded.

**ACHATINELLA APEXFULVA ROSEATA**, new subspecies

PLATE I, FIGURE 39; PLATE 6, FIGURES 25-25b

The shell is a small fossil form which looks like *A. a. lilacea* from the region of North Kaukonahua Stream. The holotype (pl. 1, fig. 39) has white, pointed, embryonic whorls; postembryonic whorls pale vinaceous fawn axially streaked and faintly spirally lined with light vinaceous fawn and vinaceous fawn; impressed sutural band white or tinted pale pinkish buff; lip outer margin pinkish buff, inner margin pale pinkish buff. Length 17.5 mm., greater diameter 11.5 mm., spire height 9.6 mm., number of whorls 6½.

Distribution, area 37?: **Waimano Stream**. "Just below the bridge on the plantation R. R.," C. M. Cooke, BBM 40679-40680, also collected by Thaanum, BBM 40716-40717, and Wilder, BBM 51932. The shells were found in fossil state under a boulder in the bottom of the gulch. I have tentatively plotted the locality somewhere in the region of area 37? (fig. 4a, p. 53).

The holotype is a little smaller than usual. The usual form should be 18+mm., with a greater diameter of 11+mm., but no specimens with the usual form have the color sufficiently well preserved to be used for the holotype. The darkest color pattern (pl. 6, fig. 25) on a single specimen has the postembryonic whorls colored light vinaceous fawn axially streaked and lined with vinaceous fawn; impressed sutural band vinaceous buff; lip vinaceous buff. Length 19.1 mm., greater diameter 11.9 mm., spire height 11.2 mm.

The narrowest specimen (pl. 6, fig. 25a) measures: Length 18.1 mm., greater diameter 10.8 mm., spire height 11.0 mm. The typical sinistral form of the shell (pl. 6, fig. 25b) measures: Length 18.0 mm., greater diameter 11.7 mm., spire height 10.4 mm.

**ACHATINELLA APEXFULVA LAURANI, new subspecies**

PLATE 1, FIGURES 37, 38; PLATE 5, FIGURES 28-31; PLATE 6, FIGURE 1

The embryonic whorls of the holotype (pl. 1, fig. 38) are white; first postembryonic and penultimate whorls, avellaneous, finely axially streaked with faint lines of bone brown, last whorl avellaneous axially streaked with olive brown and natal brown, spirally lined below the periphery with olive brown and cream buff, and banded with buffy brown, last eighth whorl bone brown; impressed sutural band natal brown; outer margin of the lip natal brown, inner margin fawn color. Length 18.2 mm., greater diameter 12.4 mm., spire height 9.7 mm., number of whorls  $6\frac{5}{8}$ .

Distribution, area 27: **Hanaiki-Waimalu Ridge**, type locality 191\*, elevation 1,200-1,250 feet, 1932; also 192, elevation 1,200-1,250 feet, Meinecke, 7 sinistral 1933 (figs. 4, 4a, p. 53). Also collected by Thurston, BBM 130604, 9 sinistral, Thwing, BBM 28751-28759, 26 sinistral.

At a lower elevation on the same ridge, possibly in the region of area 27A?, Thurston, 1910, BBM 130603, discovered a colony of dextral forms living on maile (*Alyxia*), and lehua (*Metrosidros*). Also collected by Cooke, BBM 72557-72558, 7 dextral, A. F. Judd, BBM 110492-110494 and 110496, Thwing, BBM 28986, 1 dextral.

The lightest color pattern (pl. 5, fig. 31), on 8 percent of the shells in the combined Meinecke-Thurston lots from area 27, has the postembryonic whorls white; impressed sutural and subsutural bands wood brown shading to bone brown on the last two whorls; last whorl banded and lined below and at the edge of the periphery with bister and snuff brown, about the umbilicus a band of bone brown; lip and columella callus natal brown.

The obese form of the shell (pl. 6, fig. 1) has a lined pattern which occurs on 13 percent of the shells; the first postembryonic whorl fawn color banded with white, penultimate army brown axially streaked with olive brown, and lined with white, last whorl above the periphery banded with a band of olive brown, and one of white, below the periphery a band about 5 mm. wide of cinnamon buff lined and banded with olive brown, base banded with pale pinkish buff, and a band of bister in the umbilical region. Length 18.8 mm., greater diameter 13.2 mm., spire height 9.5 mm.

A dextral shell of the usual form and color pattern from area 27A? (pl. 1, fig. 37) measures: Length 19.0 mm., greater diameter 12.4 mm., spire height 9.9 mm., number of whorls  $6\frac{1}{8}$ . The first postembryonic whorl and a half shades from fawn color to army

brown, axially streaked and finely lined with pale smoke gray, last whorl and a half bay profusely lined and streaked with tilleul buff, basal band warm sepia; outer margin of lip wood brown, inner margin vinaceous buff, columella callus white.

A narrow specimen (pl. 5, fig. 28) measures: Length 18.7 mm., greater diameter 11.3 mm., spire height 11.0 mm.; postembryonic whorls avellaneous, faintly axially streaked and spirally lined with army brown, last whorl below and at the periphery lined and banded with bister and snuff brown. An obese shell (pl. 5, fig. 29) shows a white color pattern occurring on 16 percent of the shells in the combined Cooke, Judd, and Thurston lots; postembryonic whorls white; impressed sutural band white, edged with sayal brown; last whorl below the periphery banded with light cinnamon drab, basal band fuscous. A white banded color pattern (pl. 5, fig. 30), has the postembryonic whorls white, banded with sayal brown, last whorl at and below the periphery banded with snuff brown.

In the Thurston lot (pl. 5 fig. 30a) a shell with the usual obese form has a pattern which resembles the form and type of banding of *A. a. pilsbryi*, but the color of the bands are entirely different on the two forms. The postembryonic whorls are white, last whorl banded below the periphery with chocolate; impressed sutural band chocolate. Length 18.4 mm., greater diameter 12.7 mm., spire height 9.2 mm. The presence of this chocolate-banded form in the Thurston lot is of interest, because it may be a representative of a still lower race, which is a chocolate-banded one and closely related to *A. a. pilsbryi*.

#### **ACHATINELLA APEXFULVA PARVICOLOR, new subspecies**

PLATE I, FIGURE 40; PLATE 6, FIGURES 15-15c

*Achatinella turgida ovum* PFEIFFER, Pilsbry and Cooke, Man. Conch., vol. 22, pp. 295, 298, pl. 56, figs. 3, 3a (only), 1914.

This form is smaller than *A. a. turgida* and has a light color pattern and never has the dark diamine brown or yellow color patterns of *A. a. turgida*. The subspecies is not found today, being a race collected by Gulick and identified by him as *turgida*. The embryonic whorls of the holotype (pl. 1, fig. 40) are white; postembryonic whorls pale pinkish buff, axially streaked with sayal brown, peripheral band on the last whorl pale pinkish buff; edge of the lip fawn color. Length 19.2 mm., greater diameter 12.7 mm., spire height 10.3 mm., number of whorls  $6\frac{1}{4}$ .

Distribution, area 36???: Waimalu?, Gulick. I have tentatively placed the probable locality somewhere in Waiau and Punanani

**Gulch**, because this region is often referred to as Waimalu by some collectors. The race may have come from somewhere near area 35 because the shell looks so like forms of *A. a. turgida* (fig. 4a, p. 53).

The lightest color pattern and extreme obese form (pl. 6, fig. 15) has the postembryonic whorls pale pinkish cinnamon, spotted on the first two postembryonic whorls and banded just below the impressed sutural band on the last whorl with cinnamon buff, below the periphery of the last whorl faintly lined with dots of cinnamon buff. Length 17.2 mm., greater diameter 13.0 mm., spire height 9.0 mm.

An elongate dextral (pl. 6, fig. 15a) measures: Length 18.8 mm., greater diameter 11.5 mm., spire height 10.7 mm.; embryonic whorls worn; postembryonic whorls pale pinkish cinnamon axially streaked with sayal brown, banded on the last half whorl below the periphery with a band of verona brown.

Plate 6, figure 15b, shows an obese sinistral specimen with a color pattern similar to plate 1, figure 40. An elongate sinistral (pl. 6, fig. 15c) with a color pattern similar to the holotype, measures: Length 19.1 mm., greater diameter 11.8 mm., spire height 11.0 mm.

#### GROUP OF *A. A. TURGIDA* NEWCOMB

#### *ACHATINELLA APEXFULVA OVUM* PFEIFFER

PLATE 1, FIGURE 26; PLATE 5, FIGURES 9-11

*Achatinella ovum* PFEIFFER, Proc. Zool. Soc. London, 1856, p. 334.

*Achatinella turgida ovum* PFEIFFER, Pilsbry and Cooke, Man. Conch., vol. 22, p. 297, pl. 59, fig. 17 (only), 1914.

The holotype (pl. 5, fig. 9) in the British Museum, marked with a red dot of sealing wax, is entirely white except for the black lip. Length 19.4 mm., spire height 10.3 mm., number of whorls  $6\frac{1}{4}$ . The other two shells in the type lot are white dextral specimens. One is not adult, the other (pl. 5, fig. 10) is fully developed and marked specimen A; the lip is black. Length 17.8 mm., greater diameter 12.7 mm., number of whorls  $6\frac{1}{4}$ .

Distribution, area 22: **North-Central Halawa Ridge**, locality 162C\*, elevation 1,400-1,450 feet, Meinecke, 1930 (figs. 4, 4a, p. 53). Also collected by Wilder, BBM 50525.

The holotype probably came from area 22 because that area is the lowest containing sinistral shells. The dextrals in the type lot may have come from a lower locality somewhere near area 21. Only six live shells are known to come from area 22. The colors are equally divided between the typical white *ovum* pattern of plate 1,

figure 26, and the lined pattern of plate 5, figure 11. The usual pattern (pl. 1, fig. 26) and form of the shell from area 22 has the postembryonic whorls white; about 3 mm. behind the edge of the lip the last whorl is ornamented with a streak of sayal brown and banded with a band of brownish black; lip brownish black shading to cinnamon drab on the inner edge, near the columella callus the outer edge is also cinnamon drab. Length 20.0 mm., greater diameter 13.7 mm., spire height 10.0 mm., number of whorls  $6\frac{1}{2}$ . The lined pattern (pl. 5, fig. 11) has the embryonic whorls white shading to pale pinkish buff on the first half of the first postembryonic whorl, last half pinkish buff, last two whorls pale pinkish buff banded and lined with pinkish buff and cinnamon buff, the last  $2\frac{1}{2}$  mm. behind the edge of the lip bone brown or a blackish brown; lip a blackish brown; tip of columella callus white, shading to vinaceous fawn, near the closed umbilicus. So few of the specimens were available for study that the typical form was not determined.

**ACHATINELLA APEXFULVA OVUM var. 1**

PLATE 1, FIGURE 25; PLATE 5, FIGURES 8, 8a

*Achatinella turgida ovum* PFEIFFER, Pilsbry and Cooke, Man. Conch., vol. 22, p. 298, pl. 56, fig. 10 (only), 1914.

Area 21: **North-Central Halawa Ridge**, locality 160C\*, elevation 1,000-1,100 feet, Meinecke, 1 dextral 1930; **Central Halawa** region of 162B\*, elevation 1,050-1,250 feet, Meinecke, 1914; also collected by Thurston, BBM 130505 (figs. 4, 4a, p. 53).

The shells of area 21 differ from those of area 22 in being dextral, smaller, and having an impressed sutural band of sayal brown on the first postembryonic whorl, on the remaining whorls the sutural band is white, fringed with sayal brown at the upper edge, or entirely white.

The usual form of the shell (pl. 1, fig. 25) measures: Length 18.7 mm., greater diameter 12.5 mm., spire height 9.8 mm., number of whorls  $6\frac{1}{2}$ . The shell is a dead specimen but retains most of the shell nacre; postembryonic whorls white slightly tinted with cream color just behind the edge of the lip; lip army brown.

In a fresh specimen (pl. 5, fig. 8) embryonic whorls a light shade of cream color; first postembryonic whorl cream color shading to white on the penultimate and first half of the last whorl, last half whorl above the periphery ivory yellow, last whorl below the periphery cream color lined and banded with avellaneous. Length 17.3 mm., greater diameter 12.4 mm., spire height 9.2 mm.



A narrow shell (pl. 5, fig. 8a) measures: Length 18.2 mm., greater diameter 11.8 mm., spire height 10.2 mm.; the shell is white except for the first postembryonic whorl and a half which is lined with ochraceous fawn and has the impressed sutural band ochraceous tawny; lip army brown.

**ACHATINELLA APEXFULVA OVUM var. 2**

PLATE 1, FIGURES 27, 28, 31; PLATE 5, FIGURES 12-14

Area 23: **North-South Halawa Ridge**, locality 162D\*, elevation 1,500-1,750 feet; 164D\*, elevation 1,500-1,650 feet, 5 sinistral; 165D\*, elevation 1,400-1,500 feet, 4 sinistral, all Meinecke-collected, 1930. Also collected probably in the region of areas 22 and 23 by J. S. Emerson, BBM 102211, by Dos Santos, BBM 74314, Thurston, BBM 130506, Wilder, BBM 50523 (figs. 4, 4a, p. 53).

Area 24: **Halawa-Kalauao Ridge**, locality 174\*, elevation 1,550 feet, 1930; 176-1, elevation 1,650 feet, 2 sinistral 1936; 176-2, elevation 1,700-1,750 feet, 1 sinistral 1936; 176\*, elevation 1,650-1,700 feet, 1 sinistral 1930 (figs. 4, 4a, p. 53) all Meinecke-collected. **Aiea**, J. S. Emerson, BBM 102446, 6 sinistral.

The shells of areas 23 and 24 are characterized by having certain yellow color patterns mixed with the usual *A. a. ovum* pattern of area 22.

The usual form of the shell in area 23 (pl. 5, fig. 12) measures: Length 19.4 mm., greater diameter 13.0 mm., spire height 9.5 mm.; and has a color pattern similar to that of *A. a. ovum* (pl. 1, fig. 26).

A distinctive yellow color pattern (pl. 1, fig. 27) has the embryonic whorls white; first postembryonic whorl white, impressed sutural band ochraceous tawny; first half of the penultimate whorl white, impressed sutural band light pinkish cinnamon, last half of penultimate and last whorl Naples yellow, banded at the edge of the periphery with white, impressed sutural band color of ground; lip seal brown or bone brown; columella callus fawn color. Length 19.5 mm., greater diameter 12.8 mm., spire height 10.5 mm.

In the Wilder lot (BBM 50523) of 30 shells, 50 percent are white and resemble *A. a. ovum* (pl. 1, fig. 26). The usual form of the shell (pl. 5, fig. 13) measures: Length 20.1 mm., greater diameter 13.7 mm., spire height 10.0 mm. Four shells in the lot have a yellow pattern (pl. 1, fig. 27), seven a yellow banded or lined pattern (pl. 5, fig. 11). One of the yellow-banded shells, an elongate form, has unusually dark bands (pl. 1, fig. 28). The postembryonic whorls are ochraceous tawny, finely or faintly lined with white, last whorl below the

periphery banded with a band of white, a line of ochraceous tawny, base pale pinkish buff, darkening to warm sepia behind the edge of the lip. Length 20.7 mm., greater diameter 13.1 mm., spire height 11.1 mm.

In area 24 the usual color pattern and form (pl. 1, fig. 31) is a white shell with pale pinkish buff embryonic whorls; lip and columella callus light seal brown. Length 19.2 mm., greater diameter 12.7 mm., spire height 10.0 mm. The shell is a little narrower than the usual form. The yellow-lined pattern of this area (pl. 5, fig. 14) has the postembryonic whorls white with a band of cream buff above the periphery, last whorl banded at the edge of the periphery with a band of white, below the periphery banded with chamois shading to white in the umbilical region, and lined with two lines of cinnamon.

**ACHATINELLA APEXFULVA OVUM var. 3**

PLATE 1, FIGURE 24; PLATE 5, FIGURES 6, 7

Area 20: **Moanalua-Halawa Ridge**, locality 163\*, elevation 1,500-1,620 feet, Meinecke, 9 sinistral 1930. Also collected somewhere on the same ridge by O. H. Emerson, BBM 103964, 1915 on maile (*Alyxia*) and hoe (hoi?, *Dioscorea*); J. S. Emerson, BBM 102209, 1915 (figs. 4, 4a, p. 53).

The usual color pattern of the shells in area 20 is similar to that of *A. a. ovum* (area 22), but other patterns occur which do not resemble those found in area 22. The embryonic whorls are very slightly bi-colored but are closer to *A. a. ovum* than to *A. a. simulans*.

The usual form in the Meinecke lot from locality 163\* (pl. 1, fig. 24) measures: Length 20.2 mm., greater diameter 13.2 mm., spire height 10.5 mm.; the embryonic whorls are not usual, being more pointed, first embryonic whorl light vinaceous fawn, remaining embryonic whorls white shading to pale pinkish buff; first postembryonic whorl white, lined with pinkish buff, remaining whorls white, 3 mm. behind the edge of the lip a streak of verona brown, banded with warm sepia; impressed sutural band pinkish buff shading to white on the last whorl. A peculiar pattern (pl. 5, fig. 6) has the embryonic whorls white, first embryonic whorl slightly darker than the rest; postembryonic whorls above the periphery ochraceous buff deepening to cinnamon on last half whorl, and lined on the last two whorls with white; impressed sutural band cinnamon, at and below the periphery the base is white, with a central line of cinnamon.

A third color pattern (pl. 5, fig. 7) shown on the usual form of the shell in the O. H. Emerson and J. S. Emerson lots has the postem-



bryonic whorls white, first postembryonic whorl banded with ochraceous tawny, penultimate whorl with a sutural band and a band just above the edge of the periphery of russet, last whorl lined at the edge of the periphery with buckthorn brown, subperipheral band russet, base banded with tawny; lip army brown. Length 19.5 mm., greater diameter 13.7 mm., spire height 10.0 mm.

**ACHATINELLA APEXFULVA BRUNEOLA, new subspecies**

PLATE I, FIGURE 32; PLATE 5, FIGURES 17-17b

*Achatinella turgida ovum* PFEIFFER, Pilsbry and Cooke, Man. Conch., vol. 22, p. 298, pl. 56, fig. 8a (only), 1914.

The shell resembles *A. a. ovum* in form, but differs in having a brown color pattern. Embryonic whorls of the holotype (pl. 1, fig. 32) white; first half postembryonic whorl shades from white to ochraceous tawny, penultimate and last whorl sudan brown, at the periphery and below the periphery of the last whorl the ground is argus brown, lined and banded with apricot yellow; lip verona brown; columella callus tilluel buff. Length 19.0 mm., greater diameter 13.0 mm., spire height 9.7 mm., number of whorls  $6\frac{1}{8}$ .

Distribution, area 28: **Kalauao-Hanaiki Ridge**, type locality 182, elevation 1,300-1,367 feet, Meinecke, 1926, 3 dextral 1929, 2 dextral 1933 (figs. 4, 4a, p. 53).

The holotype has the usual form of the shell, and a color pattern which occurs on 33 percent of the shells. An elongate shell (pl. 5, fig. 17) has the usual color pattern on 58 percent of the shells; postembryonic whorls ochraceous tawny spirally banded with russet, below the periphery of the last whorl prout's brown with a few lines of yellow ochre; lip and columella callus mars brown. Length 19.3 mm., greater diameter 12.2 mm., spire height 10.7 mm. A squat specimen (pl. 5, fig. 17a), with a similar color pattern to figure 17, has a very concave spire and inflated last whorl; the postembryonic whorls are profusely lined with russet. Length 19.0 mm., greater diameter 13.4 mm., spire height 8.9 mm. The lightest color pattern found on a single specimen (pl. 5, fig. 17b) has the first two postembryonic whorls pale ochraceous buff and lined with wood brown darkening to fawn color, last whorl above the periphery pale ochraceous buff lined with natal brown and buffy brown, at and below the periphery the ground is chamois above and within the aperture, the remainder of the whorl is cartridge buff; lip and columella callus army brown streaked with white.

**ACHATINELLA APEXFULVA BRUNEOLA var. 1**

PLATE 1, FIGURE 33; PLATE 5, FIGURE 18

Area 29: **Kalauao-Hanaiki Ridge**, locality 183, elevation 1,300-1,350 feet, Meinecke, 13 sinistral 1935; 183<sup>2</sup>, Meinecke, 1913 (figs. 4, 4a, p. 53).

The usual form of the shell is larger than typical *A. a. bruncola*, the mean length 20+mm. instead of 19+mm. The color pattern differs from typical *bruncola* by having the base banded with yellow; the shells are usually sinistral. The form is an intermediate one between the higher race of *A. a. aureola* and *A. a. bruncola*.

The usual form and color pattern of the shell (pl. 1, fig. 33) has the embryonic whorls white or pale pinkish buff, last two postembryonic whorls amber brown, peripheral band and base light cadmium, subperipheral band chestnut, below which are lines of amber brown and a band about the umbilicus of a deep shade of mars brown, behind the edge of the lip last whorl tinted with a streak of chestnut. Length 20.4 mm., greater diameter 13.1 mm., spire height 10.7 mm., number of whorls 6½. The color of a dextral shell (pl. 5, fig. 18) shows the light color pattern of the shell; postembryonic whorls mars yellow or a light shade of sudan brown, base cadmium with a subperipheral band of chestnut.

**ACHATINELLA APEXFULVA BRUNEOLA var. 2**

PLATE 1, FIGURE 30; PLATE 5, FIGURES 15-16

*Achatinella turgida ovum* PFEIFFER, Pilsbry and Cooke, Man. Conch., vol. 22, p. 298, pl. 56, figs. 7-7d (not from Moanalua but from Aiea, according to Dr. Cooke) and figure 6 (only), 1914 (figure 6 also matches color patterns of *A. a. ovum* var. 2).

Area 25: **Aiea-Kalauao Ridge**, locality 170C-6\*, elevation 1,550-1,800 feet, Lemke, 1924 and 1932 (figs. 4, 4a, p. 53); also collected in **Aiea** by Cooke, BBM 72501-72512, BBM 72514, BBM 16346-16347, A. F. Judd, BBM 110211-110224, Wilder, BBM 50528, 15 sinistral.

The main difference between the shells of area 25 and typical *bruncola* is that the dominant color pattern is a yellow-lined form instead of the darker usual *bruncola* pattern of plate 5, figure 17. The yellow shells are rare in area 28, whereas in area 25, 21 percent have a definitely yellow pattern without strong brown bands (pl. 5, fig. 15).

The usual form and color pattern of 37 percent of the shells (pl. 1, fig. 30) has the embryonic whorls white; first quarter postembryonic whorl white, next quarter tawny lined with pale pinkish buff, penulti-

mate cream buff lined with tawny, last whorl antimony yellow lined above the periphery with tawny, below and at the periphery with chestnut; lip warm sepia, columella callus white. Length 18.7 mm., greater diameter 12.5 mm., spire height 9.6 mm., number of whorls  $6\frac{1}{4}$ .

Eight percent are dark brown above the periphery and yellow below (pl. 5, fig. 15a); the postembryonic whorls tawny faintly lined or tinted with warm buff, banded above and below the periphery with chestnut, below and at the periphery the ground is naples yellow. The typical form of a shell of the 19+ mm. length class (pl. 5, fig. 15) measures: Length 19.7 mm., greater diameter 13.6 mm., spire height 10.0 mm.; postembryonic whorls shade from white to light buff on the last half of the penultimate, last whorl above the periphery white, tinted with light buff, finely spirally lined with faint lines of chamois, below the periphery ground is mustard yellow within the aperture lightening to naples yellow, and spirally lined with buckthorn brown, except behind the edge of the lip where the bands and lines are russet; impressed sutural band russet. The lightest yellow pattern (pl. 5, fig. 15b) has the postembryonic whorls white up to the last whorl which is mustard yellow with a line of ochraceous tawny at the edge of the periphery.

The dextral race of *bruneola* var. 2 is probably a remnant of two races. The lower, a brown race similar to typical *A. a. bruneola*, may possibly have been a pure one and not mixed with the yellow or upper form similar to *A. a. aureola*. Above the brown race yellow forms existed, and locality 170C-6 is the point where the two races overlapped.

The Wilder lot, BBM 50528, may indicate that a yellow race occurs between areas 24 and 25. The shells were probably collected over a wide area inclusive of area 24 because of the presence of white shells; and above area 25 because no dextrals are found in the lot. One specimen has a brown color pattern (pl. 5, fig. 16); postembryonic whorls white, banded on the first postembryonic whorl with tawny, last whorl banded with chestnut. Thirty-three percent have a yellow pattern similar to that of plate 5, figure 15. Sixty percent have whitish color patterns similar to those of plate 1, figure 31, and plate 5, figure 6. The yellow shells are probably a sinistral race of *A. a. aureola*, but because the locality is not definite, the range of color variation is not known and these shells have therefore been lumped with *A. a. bruneola* var. 2 until more data are obtainable. In like manner the white forms are probably *A. a. ovum* var. 2.

**ACHATINELLA APEXFULVA AUREOLA, new subspecies**

PLATE I, FIGURES 34, 35; PLATE 5, FIGURES 19-21a

*Achatinella turgida ovum* PFEIFFER, Pilsbry and Cooke, Man. Conch., vol. 22, p. 298, pl. 56, fig. 8 (only), 1914.

The shell is obese and resembles *A. a. bruneola* in form, but differs in the color pattern, having a yellow ground usually lightly banded with brown. The embryonic whorls of the holotype (pl. 1, fig. 34) are white; first postembryonic whorl pale pinkish buff axially streaked with sayal brown, penultimate whorl pale pinkish buff axially streaked with ochraceous tawny; impressed sutural band ochraceous tawny, last whorl above the periphery pale pinkish buff, banded at edge of the periphery and above the periphery with a band 2.8 mm. wide, amber brown above the aperture, the band is lined with mustard yellow, and on the last half whorl breaks up into three bands of amber brown, just behind the edge of the lip a streak of warm sepia, last whorl below the periphery mustard yellow; lip army brown streaked with white; columella callus army brown shading to white at the tip of the callus. Length 20.4 mm., greater diameter 14.1 mm., spire height 9.8 mm., number of whorls  $6\frac{1}{2}$ .

Distribution, area 30: **Kalauao-Hanaiki Ridge**, type locality 184, elevation 1,350-1,450 feet, 1926, also 1913, 7 sinistral 1929, 8 sinistral 1935; 185, elevation 1,450-1,500 feet, 1933; 187, elevation 1,600 feet, 1933; 187?, 1932; 188, elevation 1,650-1,700 feet, 1 sinistral 1933, all Meinecke-collected (figs. 4, 4a, p. 53).

The form of the shell in locality 184 may be more elongate (pl. 5, fig. 20) and have a darker spire than the holotype. Length 20.2 mm., greater diameter 13.0 mm., spire height 10.6 mm. Last half of first postembryonic whorl, penultimate, and last whorl above the periphery tawny buff, lined, banded, and streaked with a shade of color between ochraceous tawny and avellaneous; impressed sutural band same color; last whorl at the edge of the periphery banded with tawny, below the periphery mustard yellow and with a line of tawny, behind the edge of the lip a streak of black. A single specimen (pl. 5, fig. 19) has a white spire; last whorl below and just above the periphery Naples yellow, banded with white at the edge of the periphery, below the periphery banded with amber brown, just behind the edge of the lip a streak of black.

The lightest color pattern in locality 185 (pl. 5, fig. 20a) has white postembryonic whorls, banded and lined with tawny and ochraceous tawny, last half whorl banded at the edge of the periphery with Mars brown, behind the edge of the lip a streak of black or Mars brown.

The dextral shells of locality 187 are not so obese as those of locality 184. The usual form and pattern of a dextral (pl. 1, fig. 35) measures: Length 19.8 mm., greater diameter 12.4 mm., spire height 10.5 mm., embryonic whorls white; postembryonic whorls shade from cream color to naples yellow on the last whorl, last whorl below the periphery mustard yellow, banded at the edge of the periphery with a faint band of ochraceous tawny, below the periphery with tawny, behind the edge of the lip a streak of black.

The obese and banded form of the shell (pl. 5, fig. 21) measures: Length 18.9 mm., greater diameter 13.3 mm., spire height 8.8 mm. Postembryonic whorls mustard yellow, faintly lined on the last whorl above the periphery with cinnamon buff; impressed sutural band russet; last whorl at the periphery and below banded with ochraceous tawny, russet and mars brown about the base, behind the edge of the lip a streak 2 to 3 mm. wide of black. A narrow elongate form and a yellow color pattern (pl. 5, fig. 21a) has the postembryonic whorls naples yellow deepening to yellow ochre on the last whorl, lined above the periphery of the last whorl with naples yellow. Length 20.2 mm., greater diameter 12.0 mm., spire height 11.1 mm.

There is some doubt in my mind concerning the accuracy of some of the material collected by Meinecke in localities 184 and 187. After comparing the material with his more recently collected shells found after 1933, I believe that the early lots of shells collected prior to 1933, and plotted from memory, have been misplotted. I have taken the liberty of arranging the sequence of areas in a probably correct order, taking the 1933 and later collected material to be correct. In doing so I may have made an error, and I hope that some student of Hawaiian tree snails may check the order of color variations on this ridge. The change in form from narrow dextral shells in area 28 to sinistral obese ones in locality 184 and finally to narrow dextrals again in locality 187 is most interesting if true. On the variation of form, one would be led to suppose that the sequence is area 28, locality 187, area 29, locality 184, and finally locality 185, locality 188, and area 31.

In locality 185 the color pattern and form of the shells is similar to that of locality 184, the only difference being that a few specimens (3 out of 10) have a white ground in locality 185, while in area 184 no white color patterns occur. The single shell from 188 has an entirely yellow color pattern. I have considered this locality the borderline extremity of the typical *aureola* area with a few specimens showing the lighter color patterns of area 31.



**ACHATINELLA APEXFULVA AUREOLA var. 1**

PLATE 1, FIGURE 36; PLATE 5, FIGURES 22-22b

Area 31: **Kalauao-Waimalu Ridge**, locality 190A\*, elevation 1,750-1,800 feet, 1932; 191A\*, elevation 1,600 feet, 5 sinistral 1932, all Meinecke-collected (figs. 4, 4a, p. 53).

The color pattern of the shells in this sector are white shells banded or tinted with yellow or banded with brown. A usual pattern in locality 190A\* (pl. 5, fig. 22) has the postembryonic whorls white, the last half of the first postembryonic whorl and the first half of the penultimate faintly lined and banded with tawny, the last half of the penultimate faintly banded and lined with cream buff, the first half of the last whorl mustard yellow with a peripheral band and supraperipheral line of buckthorn brown, last half whorl white tinted with mustard yellow, with the peripheral band buckthorn brown, behind the edge of the lip a streak of mars brown. A brown color pattern (pl. 5, fig. 22a) has the postembryonic whorls above the periphery antimony yellow axially streaked and lined with amber brown; impressed sutural band chestnut; last whorl and a half at the edge of the periphery and below the periphery white tinted with cream color, in the umbilical region a patch of amber brown. A white color form (pl. 5, fig. 22b) resembles *A. a. ovum*. The entire shell is white, tinted on the last whorl with mustard yellow, last fourth whorl faintly banded with mustard yellow, behind the edge of the lip mars brown.

In the higher locality of 191A\*, the usual color pattern (pl. 1, fig. 36) is a white shell banded on the last whorl above the periphery and all below the periphery with mustard yellow. The shells in the upper region are all sinistral; in 190A\* they are all dextral.

**ACHATINELLA APEXFULVA WAIMALUENSIS, new subspecies**

PLATE 1, FIGURE 45; PLATE 5, FIGURES 25, 25a

The shell looks like a form of *A. a. ovum* or *A. a. aureola* and their varieties, but is distinct from them in having the first postembryonic whorl banded with brown so that the whorl stands out, being darker than the whorls above and below it. The *A. a. ovum* and *A. a. aureola* forms have a color pattern which usually darkens consistently on the later whorls.

The embryonic whorls of the holotype (pl. 1, fig. 45) are cartridge buff; first postembryonic whorl banded on the lower portion of the whorl with ochraceous tawny, the band decreasing from three-fourths the width of the whorl to half its width, on the white penultimate and



last whorl the band narrows to a line and fades from ochraceous tawny to a light shade of ochraceous tawny; below the periphery of the last whorl the shell is banded with a light shade of ochraceous tawny, base cream color; lip russet; columella callus light vinaceous fawn. Length 20.7 mm., greater diameter 13.1 mm., spire height 11.4 mm., number of whorls  $6\frac{1}{2}$ .

Distribution, area 32: **Waimalu-South Central Waimano Ridge**, type locality 204C, elevation 1,660 feet, Meinecke, 6 sinistrals 1933; also 202C, elevation 1,500-1,550 feet; 203C, elevation 1,600-1,660 feet; 206C, elevation 1,600 feet, Meinecke, 1 sinistral 1933 (figs. 4, 4a, p. 53).

The darkest color pattern (pl. 5, fig. 25) has the first half post-embryonic whorl banded on the lower half of the whorl with a light shade of clay color lined with white and fading to white on the last half of the whorl, the penultimate whorl is white, lined on the lower portion just above the edge of the periphery with honey yellow shading to chamois, the last whorl is chamois all below the periphery and just above the periphery, the remainder of the shell is white, below the periphery banded with tawny.

The lightest pattern (pl. 5, fig. 25a) has the last two whorls white, tinted and faintly spirally banded with naples yellow, behind the edge of the lip a streak or axial stripe of black.

#### ACHATINELLA APEXFULVA WAIMALUENSIS var. 1

##### PLATE I, FIGURE 44

Area 32A: **South Central Waimano-Central Waimano Ridge**, locality 202D, elevation 1,400 feet; 203D, elevation 1,450 feet, Meinecke, 1933 (figs. 4, 4a, p. 53). Only one live specimen has been collected in area 32A. The other shells are such dead specimens that the range of color patterns is not known.

The color pattern on the live shell (pl. 1, fig. 44) from locality 202D is a shell with a color pattern similar to *A. a. waimaluensis* (pl. 5, fig. 25), except that the spire is banded. The first embryonic whorl is broken off, the remaining embryonic whorls light buff; postembryonic whorls white, banded with ochraceous tawny, lower half of last whorl naples yellow with a line of ochraceous tawny at the edge of the periphery, on the last half whorl three bands of warm sepia; lip not formed; columella callus pale vinaceous fawn. The color pattern is intermediate between *A. a. simulacrum* and *A. a. waimaluensis*, but closest to *waimaluensis*.

## ACHATINELLA APEXFULVA TURGIDA Newcomb

PLATE 1, FIGURE 41; PLATE 6, FIGURES 2-10

*Achatinella turgida* NEWCOMB, Proc. Zool. Soc. London, 1853, p. 134, pl. 22, figs. 10-10a.—PILSBRY and COOKE, Man. Conch., vol. 22, p. 294, pl. 29, figs. 10-10a; pl. 56, figs. 1-2, 4, 11 (only), 1914.

*Achatinella swiftii* NEWCOMB, Proc. Zool. Soc. London, 1853, p. 133, pl. 22, figs. 9, 9a.—PILSBRY and COOKE, Man. Conch., vol. 22, p. 306, pl. 29, figs. 9, 9a (only), 1914.

Newcomb's description of *A. a. turgida* may refer to either of his original figures. I shall choose his figure 10 (pl. 6, fig. 2) to be the lectotype, because it has the most usual pattern. The original specimen (pl. 6, fig. 3) of Newcomb's figure 10 has white embryonic whorls; penultimate and last postembryonic whorls pallid mouse gray, axially spotted and spirally banded with hessian brown, on the last whorl near the middle of the whorl there are three axial bands of cinnamon, behind the edge of the lip an axial band of hessian brown, in the umbilical region below the last hessian brown band the ground is cream buff, mixed with pallid mouse gray; impressed sutural band hessian brown; lip and columella callus light vinaceous fawn. Length 19.7 mm., greater diameter 13.4 mm., spire height 10.9 mm., number of whorls  $6\frac{1}{4}$ .

Distribution, area 35: **Waiau-South Waimano Ridge**, locality 200B\*, elevation 850-1,000 feet, 7 dextral, 1 sinistral 1929; 202B, elevation 1,000-1,150 feet, 1913, 1 dextral, 8 sinistral 1914, 1920, 7 dextral, 2 sinistral 1929, 12 dextral, 1 sinistral 1932, 1934; 202BB\*, elevation 1,050-1,150 feet, 5 dextral, 1 sinistral 1929, all collected by Meinecke. **Waimano**, Wilder, BBM 50598; **Waimalu**, J. S. Emerson, BBM 102218. Pilsbry and Cooke report *A. a. turgida* to have been taken in Waiawa by I. Spalding. This is an error, for no *A. a. turgida* are found except in the region of Waimalu to Waimano (figs. 4, 4a, p. 53). Holotype in BM marked with an x.

The usual form and color pattern (pl. 1, fig. 41) of *A. a. turgida* in area 35 is very much like the lectotype in color. The shell measures: Length 19.0 mm., greater diameter 13.2 mm., spire height 10.1 mm., number of whorls  $6\frac{1}{2}$ . The embryonic whorls are white; postembryonic whorls diamine brown, splotted and banded with broken bands of pale smoke gray tinted with chamois; impressed sutural band diamine brown; lip and columella callus pale vinaceous fawn.

The darkest or reddish-brown color pattern and narrow form of the shell (pl. 6, fig. 4) has the postembryonic whorls diamine brown and looks like a sinistral specimen of *A. a. apexfulva* which has white embryonic whorls instead of yellow ones. Length 19.5 mm., greater diameter 12.6 mm., spire height 10.0 mm.

The usual yellow pattern and obese form of the shell (pl. 6, fig. 4a) has the first half postembryonic whorl ochraceous tawny banded on the lower half of the whorl with pale ecru drab, remaining whorls chamois splotched with snuff brown, hessian brown, and saccardo's umber, suprapерipheral band on the last whorl warm sepia, last whorl below the periphery ornamented with zigzag streaks of snuff brown; impressed sutural band warm sepia. Length 19.4 mm., greater diameter 14.5 mm., spire height 9.7 mm.

The lightest or yellowish white color pattern (pl. 6, fig. 4b) has the postembryonic whorls white, on the first quarter whorl a patch of mars brown, remaining whorls streaked with ochraceous tawny; impressed sutural band on the first postembryonic whorl and a half diamine brown, last whorl and a half the sutural band is the color of the whorl below; lip light vinaceous fawn.

The typical form of a dextral shell and a variant of the yellow color pattern is figured on plate 6, figure 4c; first two postembryonic whorls pale gull gray, axially streaked with zigzag lines of neutral gray and deep neutral gray, and ochraceous tawny, last whorl cartridge buff tinted with cream color streaked with white and with axial splotches of ochraceous tawny, prout's brown, and mars brown. Length 19.5 mm., greater diameter 13.7 mm., spire height 9.4 mm.

A characteristic gray color pattern (pl. 6, fig. 4d) is also found in all *turgida* localities; the postembryonic whorls are pale gull gray spirally banded lined and splotched with diamine brown. The yellow color pattern (pl. 6, fig. 4e) may lack or have very little axial splotching; the first two postembryonic whorls are cartridge buff tinted with deep olive buff, last whorl chamois spirally lined and banded with chestnut and faintly axially streaked on the last half whorl with chestnut.

The size of the dextral shells varies from narrow specimens (pl. 6, fig. 5) to obese forms (pl. 6, fig. 6). The shell of figure 5 is a peculiar rare color pattern of the reddish-brown form, having a subperipheral chamois band faintly streaked with tawny on the last whorl, the remaining postembryonic whorls diamine brown; outer margin of lip army brown shading to white on the inner margin; columella callus white. Length 19.1 mm., greater diameter 12.5 mm., spire height 10.6 mm. The obese form of figure 6 measures: Length 19.2 mm., greater diameter 14.1 mm., spire height 9.6 mm.; the postembryonic whorls diamine brown spirally lined with apricot yellow on the penultimate, and banded and lined on the last whorl with mars yellow, light buff, or antimony yellow, which bands are axially streaked and lined with diamine brown or mouse gray.

The specimens used by Newcomb for his original figures of *A. swiftii* were not located in the British Museum. One lot labeled the type of *A. swiftii* contained shells which do not match the original figures, and are forms of *A. a. perplexa*.

Newcomb's figure 9 (pl. 6, fig. 7) closely matches yellow forms splotched with brown of *A. a. turgida* (pl. 6, fig. 4c). In the Newcomb collection at Cornell University there is a specimen of *A. a. turgida* (pl. 6, fig. 9) which closely resembles Newcomb's figure 9. Plate 6, figure 10, shows a specimen which looks very much like Newcomb's figure 9a (pl. 6, fig. 8), the postembryonic whorls are diamine brown, penultimate whorl is lined with white, last whorl banded below the periphery with yellow ochre, with a line of diamine brown near the center of the band; lip light vinaceous fawn.

Since *A. swiftii* so closely resembles patterns of *A. a. turgida* I consider it to be a synonym of *turgida*. *A. swiftii* has page priority over *A. a. turgida* but I am reluctant to make *turgida* a synonym of *swiftii* since the type of *swiftii* has not been located and the type of *turgida* has. Moreover, since the original figures do not match the original description, there is some doubt about the exact identification of *A. swiftii*. Therefore it is best to put *swiftii* in the synonymy of *A. a. turgida*.

#### ACHATINELLA APEXFULVA MEADOWSI, new subspecies

PLATE I, FIGURE 42; PLATE 6, FIGURES 11-12

*Achatinella turgida ovum* PFEIFFER, Pilsbry and Cooke, Man. Conch., vol. 22, p. 298, pl. 56, fig. 9 (only); pl. 56, fig. 12 (an intermediate form between *A. a. meadowsi* and *A. a. turgida* but closest to *meadowsi*), 1914.

The shell of the holotype (pl. 1, fig. 42) is a yellow-brown form of *A. a. turgida* differing mainly in color pattern; the embryonic whorls pale pinkish buff; postembryonic whorls yellow ochre heavily banded on the first two whorls and above the periphery of the last whorl with amber brown, below the periphery the amber brown bands are faint so that the color is mostly yellow ochre, in the umbilical region a band of black; impressed sutural band warm sepia or black; lip army brown; columella callus light vinaceous fawn; behind the edge of the lip a streak of black. Length 19.6 mm., greater diameter 13.7 mm., spire height 9.6 mm., number of whorls  $6\frac{1}{2}$ .

Distribution, area 34: **South Waimano-South Central Waimano Ridge**, type locality 212b, elevation 1,300 feet; 213a-213b, elevation 1,350-1,400 feet, 17 sinistral; 213a, elevation 1,350 feet, all collected by Meinecke, 1933. Meadows and Welch (BBM 107555-



107556) collected this form on the Waiau-South Waimano Ridge somewhere above area 35. The exact locality was not plotted, so is not being used in this paper (figs. 4, 4a, p. 53).

*A. a. meadowsi* is found in the Meinecke lots of *A. a. turgida* from area 35, but only a few specimens in the different lots, and some lots entirely lack this color form. Area 35 of *A. a. turgida* is probably a borderline area between *A. a. meadowsi* and a distinct pure race of *A. a. turgida*. The subspecies is named after E. J. Meadows, of Honolulu.

The elongate form (pl. 6, fig. 11) measures: Length 20.0 mm., greater diameter 12.5 mm., spire height 11.0 mm.; postembryonic whorls yellow ochre lightly streaked, banded, and lined with ochraceous tawny, last whorl banded at and below the periphery with warm sepia, or black; impressed sutural band warm sepia or black.

The darkest color pattern (pl. 6, fig. 11a) has the postembryonic whorls carob brown banded on the last whorl and a half with a band of yellow ochre which is lined and streaked with ochraceous tawny.

An obese specimen (pl. 6, fig. 12) with the postembryonic whorls yellow ochre and very faintly lined and banded with ochraceous tawny, measures: Length 19.0 mm., greater diameter 14.0 mm., spire height 9.3 mm.

#### ACHATINELLA APEXFULVA MEADOWSI var. 1

##### PLATE 6, FIGURES 13-14a

In locality 213a (fig. 4, p. 53) two specimens are found which did not have the usual glossy surface of typical *A. a. meadowsi*, but have a very dull appearance. The postembryonic whorls (pl. 6, fig. 13) are pale pinkish buff spirally banded and lined with ochraceous tawny; impressed sutural band warm sepia or black.

Wilder (BBM 50537) obtained from somewhere in the Waimano region a series of the shells all of which are dull forms. The color pattern ranges from dark patterns such as plate 6, figure 14, to light ones such as plate 6, figure 14a. The dark color pattern has the postembryonic whorls chestnut streaked with antimony yellow, sub-peripheral band light buff with a central band of ochraceous tawny; impressed sutural band warm sepia. The light pattern (pl. 6, fig. 14a) is colored on the first postembryonic whorl with pinkish buff; impressed sutural band pinkish buff; banded in the umbilical region with snuff brown.

This dull form may be a variety of *A. a. meadowsi* which occurs on the Waimalu-South Waimano Ridge or somewhere between areas

34 and 35. The dull race as can be noted above has a wider range of color pattern than typical *A. a. meadowsi*.

**ACHATINELLA APEXFULVA MEADOWSI** var. 2

PLATE I, FIGURE 43; PLATE 5, FIGURES 23, 24

Area 33: Waimalu-South Central Waimano Ridge, locality 200Ca, elevation 1,200-1,350 feet, 1932; 200C, elevation 1,400 feet, 2 sinistrals 1933; 201Ca, elevation 1,250-1,400 feet, 10 sinistrals 1933; 201C, elevation 1,450 feet, 1933, all collected by Meinecke (figs. 4, 4a, p. 53). This form also collected by J. S. Emerson (BBM 102229).

From the dark brown *meadowsi* forms of area 34 the shells become much lighter in shade the higher the locality. Area 33 is really an intermediate one between the light color pattern of *A. a. waimaluensis* and *A. a. meadowsi*, but is closest to *meadowsi* in color pattern.

The usual color pattern (pl. 1, fig. 43) has the embryonic whorls light buff lightening to pale pinkish buff lined with white; first post-embryonic whorl pale pinkish buff lined with pinkish buff, penultimate whorl cream color, subsutural band light ochraceous buff, last whorl mustard yellow tinted with buckthorn brown; the impressed sutural band on the first postembryonic whorl shades from mikado brown to warm sepia, on the penultimate whorl the upper portion of the sutural band is banded with warm sepia, the lower half is that of the ground color, the width of the warm sepia band narrows continually so that on the last whorl only a fringe of warm sepia exists on the upper portion of the band; lip vinaceous brown; columella callus light vinaceous fawn.

The lightest color pattern (pl. 5, fig. 24) is pale pinkish cinnamon, tinted on the last whorl with faint lines of warm buff; impressed sutural band russet lightening to avellaneous on the last whorl. A pattern (pl. 5, fig. 23) that looks like a light form of *A. a. meadowsi* also occurs; postembryonic whorls maize yellow spirally lined or banded with a light shade of clay color or a yellowish shade of ochraceous tawny.

**ACHATINELLA APEXFULVA PERPLEXA** Pilsbry and Cooke

PLATE I, FIGURE 47; PLATE 6, FIGURES 16-19d

*Achatinella turgida perplexa* PILSBRY and COOKE, Man. Conch., vol. 22, p. 296, pl. 56, figs. 5-5d (only), 1914.

To quote from Pilsbry and Cooke:

The shell has a white ground indistinctly streaked with pale neutral gray, and encircled with numerous lines and bands of darker gray or olive brown. First



embryonic whorl cartridge-buff with the tip either white or a little darkened, bluish or fleshy, the rest of the embryonic whorls white. First neanic whorl often marked with brown. The lip is vinaceous pink or light brownish vinaceous, fading on the rather strong lip-rib. About 6 percent are sinistral.

Length 20.7 mm., diam. 13.6 mm.,  $6\frac{1}{3}$  whorls.

Length 18.0 mm., diam. 12 mm.

Lateral spurs, and northern ridge of Waimano Valley, C. M. Cooke. Cotypes, 1192 Cooke coll. and 108802 A.N.S.P.

The grayish color and pale lip are the chief characters of this race, of which there are about 130 specimens in Dr. Cooke's collection. It varies a good deal. The bluish-gray streaks are often absent, or visible only on the bands, and the latter vary from light to dark. The sutural margin is usually touched faintly or distinctly with tawny. Figures 5, 5a are typical patterns.

Distribution, area 40: **Waimano-Manana Ridge**, locality 221 $\frac{1}{2}$ \*, elevation 1,050-1,100 feet, 1926; 222\*, elevation 1,100-1,150 feet, 1929, both collected by Meinecke (figs. 4, 4a, p. 53). Cooke's type locality in **Waimano** probably extends over areas 40 and 44, because the type lot (BBM 72723-72753) contains a mixture of the typical *perplexa* patterns of area 40 and the *nigripicta* var. 1 patterns which in the Meinecke collection are limited to area 44. Other collectors of this form are Wilder, BBM 50550-50551, and J. S. Emerson, BBM 102243. The Emerson lot is dominantly from the upper region of area 44, while the Wilder lots come mostly from the lower area 40. Both lots have many intermediate forms the patterns of which would identify them with either area.

Pilsbry's plate 56, figure 5, is considered the lectotype and is reproduced in this paper on plate 6, figure 16. The figure is slightly larger in proportion to the other figures. All the typical *perplexa* forms of the original Cooke lot are studied. The usual form (pl. 1, fig. 47) and gray pattern on about 55 percent of the shells has the embryonic whorls white; first half postembryonic whorl pale pinkish buff axially streaked with cinnamon, remaining postembryonic whorls white finely axially streaked and lined with light drab or a shade between light drab and tawny olive, peripheral band on last whorl white; impressed sutural band a faint shade of tawny olive; lip and columella callus seashell pink. Length 18.4 mm., greater diameter 12.8 mm., spire height 10.0 mm.

A variant of the typical color pattern, which may be considered a grayish pattern (pl. 6, fig. 17), has the first half postembryonic whorl sayal brown banded with a line of pale pinkish buff, last half verona brown; penultimate whorl drab streaked and tinted with benzo brown on the first half of the whorl, lower fourth of the whorl banded with pale gull gray, last whorl pale gull gray axially streaked with white,

spirally banded above the periphery with a band of pale pinkish buff axially streaked with drab, peripheral line fuscous, subperipheral band warm sepia streaked with hair brown and smoke gray, basally lined with sepia; spire concave in outline.

The grayish color pattern (pl. 6, fig. 18) may be more lined than figure 17; first postembryonic whorl mikado brown, faintly lined with pale pinkish buff, penultimate whorl ground pale pinkish buff covered with close-set axial streaks of drab, cinnamon drab and benzo brown, spirally lined with fuscous, last whorl pale pinkish buff, banded above the periphery with a light drab band which is lined with olive brown, banded at the periphery with olive brown, below the periphery with hair brown, lined with fuscous, lip light vinaceous fawn. This pattern collected by Meinecke in area 40 is also found in the Cooke lots.

Brownish color patterns are depicted on plate 6, figures 17*a*, 17*b*. Figure 17*a* is an extreme elongate specimen, with the spire straight in outline. Length 19.2 mm., greater diameter 11.8 mm., spire height 11.1 mm. Postembryonic whorls mikado brown, spirally lined and faintly streaked with zigzag streaks of tilleul buff, peripheral band tilleul buff lined with vinaceous buff. Figure 17*b* is a darker color pattern and the obese form of the shell. Length 19.8 mm., greater diameter 13.5 mm., spire height 11.0 mm. First postembryonic whorl cream color, with impressed sutural band ochraceous tawny, last two whorls army brown streaked with pale smoke gray.

Meinecke found a white sinistral specimen in locality 221½\* (pl. 6, fig. 18*a*) the postembryonic whorls white, first two postembryonic whorls lined with pinkish buff, last whorl lined with cinnamon buff.

While the paratype Cooke lots are all dextral, 46 percent of the shells in the Wilder collection are sinistral. These sinistrals have a different color pattern range from those collected by Cooke. Yellowish or pink color patterns occur. The usual form and color pattern of 50 percent of the sinistrals (pl. 6, fig. 19) has the embryonic whorls pale pinkish buff; first half postembryonic whorl pale pinkish buff, axially streaked with sayal brown, next half whorl streaked with army brown, penultimate and last whorl light drab axially streaked with hair brown, and banded below the suture with white, last whorl below the periphery white with two lines of benzo brown. Length 18.1 mm., greater diameter 12.3 mm., spire height 9.4 mm.

A variant (pl. 6, fig. 19*a*) of the typical gray color pattern has the first half of the first postembryonic whorl ochraceous tawny, last half russet, penultimate tawny olive lined with smoke gray, last whorl smoke gray spirally lined with tawny olive. It is an obese form. Length 18.2 mm., greater diameter 13.3 mm., spire height 9.4 mm.

Twenty-two percent have a yellow ground (pl. 6, fig. 19*b*) the last two whorls cream color with bands of buffy brown which are axially streaked with natal brown. Eleven percent are pinkish patterns. The darkest of these (pl. 6, fig. 19*c*) has the postembryonic whorls colored pinkish cinnamon. The lightest pink pattern (pl. 6, fig. 19*d*) is sea-shell pink axially streaked with onion-skin pink, and spirally banded and lined on the last whorl with pale vinaceous fawn.

**ACHATINELLA APEXFULVA COOKEI Baldwin**

PLATE I, FIGURE 49; PLATE 7, FIGURES 7-10, 12-12*d*

*Achatinella cookei* BALDWIN, Proc. Acad. Nat. Sci. Philadelphia, 1895, p. 220, pl. 10, fig. 15.

*Achatinella turgida cookei* BALDWIN, Pilsbry and Cooke, Man. Conch., vol. 22, p. 300, pl. 57, figs. 15-17, 1914.

Distribution, area 45: **Waimano-Manana Ridge**, locality 225\*, elevation 1,300-1,400 feet, 35 sinistral 1929; 225-1, elevation 1,500 feet, 2 dextral 1933; 226\*, elevation 1,300-1,426 feet, 15 dextral 1929, all collected by Meinecke (figs. 4, 4*a*, p. 53). Type lot BBM 167352 of 8 dextral, collected by C. H. Cooke and labeled **Ewa**. The D. D. Baldwin lot, BBM 54669, of 4 dextral, was obtained from C. H. Cooke. Type locality on the **Waimano-Manana Ridge** was later collected by C. M. Cooke, Jr., BBM 72697-72698, 4 dextral, 4 sinistral, and R. A. Cooke, BBM 58340, 7 dextral and 2 sinistral. Probably the later collections include a slightly different region than the type locality, because the type lots contain no sinistrals. Also collected by Wilder, in **Waimano**, BBM 50594-50595, 142 sinistral, and 13 dextral.

The exact location of the type locality has not been plotted, but the color patterns in the type lot in the Bishop Museum closely match those of the shells from area 45. The shell Baldwin used for his original figure cannot be found in either the Bishop Museum or the Academy of Natural Sciences of Philadelphia.

A shell in the Academy of Natural Sciences, figured on plate 7, figure 8, more closely approximates the form of Baldwin's figure reproduced on plate 7, figure 7, but differs in size, thickness of the lip, and in having a band of pinkish buff in the umbilical region. The embryonic whorls of figure 8 are white shading to cartridge buff on the last half embryonic whorl; postembryonic whorls pinkish buff, last whorl spirally lined with lines darker than the ground, on the last half whorl a band of white at the periphery, below the periphery

last whorl hessian brown; lip and columella callus light vinaceous fawn. Length 19.4 mm., greater diameter 14.2 mm., number of whorls 6. While the shell of figure 8 does not match the original figure and measurements in all details, it comes from what is supposed to be the type lot and best matches the form of Baldwin's original figure. This shell is therefore considered the lectotype.

The usual form of the shell selected from the original type lot collected by C. H. Cooke is shown on plate 7, figure 9; the embryonic whorls white; postembryonic whorls pale pinkish buff tinted with light buff, lower half of last whorl a dark shade of diamine brown or dark livid brown. Length 19.2 mm., greater diameter 13.4 mm., spire height 9.8 mm. A narrow specimen (pl. 7, fig. 10) obtained in the type lot has the postembryonic whorls white, with the base warm blackish brown. Length 19.5 mm., greater diameter 12.8 mm., spire height 10.4 mm.

Plate 1, figure 49, shows a dextral specimen from locality 225-1. The postembryonic whorls are white, last whorl lower half warm blackish brown. Length 19.5 mm., greater diameter 12.8 mm., spire height 10.6 mm., number of whorls  $6\frac{1}{2}$ .

The range of color patterns in the Wilder collection is shown on plate 7, figures 12-12d. All with the exception of the shell of figure 12d have the lower half of the last whorl a deep shade of diamine brown or warm blackish brown. The usual form and color pattern (pl. 7, fig. 12) has the postembryonic whorls white, tinted with ochraceous tawny; impressed sutural band ochraceous tawny. Length 18.3 mm., greater diameter 12.3 mm., spire height 9.7 mm. An elongate shell (pl. 7, fig. 12a) with an entirely white spire measures: Length 19.6 mm., greater diameter 12.3 mm., spire height 10.9 mm.

Thirty-six percent have a definitely yellow pattern. The usual form and color pattern of one of the yellow shells (pl. 7, fig. 12b) has the embryonic whorls cartridge buff; postembryonic whorls ochraceous tawny with an impressed sutural band of tawny. Length 19.0 mm., greater diameter 12.4 mm., spire height 9.9 mm. An obese shell and a lined form of the yellow pattern (pl. 7, fig. 12c) measures: Length 18.2 mm., greater diameter 13.1 mm., spire height 9.5 mm.; last two postembryonic whorls ochraceous tawny streaked with tawny and finely spirally lined with white. Five shells of the yellow pattern lack the typical dark *cookei* base. One of these (pl. 7, fig. 12d) has the postembryonic whorls light buff, faintly axially streaked or tinted ochraceous tawny; impressed sutural band ochraceous tawny.

**ACHATINELLA APEXFULVA COOKEI** var. 1

PLATE 1, FIGURE 46

Area 39: **North Central Waimano-North Waimano Ridge**, locality 211B, elevation 1,350-1,425 feet; 212B, elevation 1,400 feet, 1 dextral, 3 sinistral; 213B, elevation 1,350-1,450 feet, 2 dextral; 214B, elevation 1,500-1,560 feet, 9 dextral, all Meinecke-collected, 1933 (figs. 4, 4a, p. 53).

The shells of area 39 have a series of color patterns similar to those of the shells of area 45. The only reason for separating the two areas is that a few shells occur in area 39 which do not have the usual solid dark base of typical *A. a. cookei* and differ from the patterns found in area 45. The shell may be white (pl. 1, fig. 46) with a single band of black or warm blackish brown below the periphery of the last whorl. One white specimen with a vinaceous fawn lip and a patch of black behind the edge of the lip, below the periphery, was found in locality 214 B.

**ACHATINELLA APEXFULVA COOKEI** var. 2

PLATE 1, FIGURE 56; PLATE 7, FIGURES 11-11b

Area 49: **Manana-Waiawa Ridge**, locality 237f, elevation, 1,700 feet; 237fa, elevation 1,500-1,600 feet, Meinecke 1933 (figs. 4, 4a, p. 53).

Sandwiched in between *A. a. nigripicta* (area 50), and *nigripicta* var. 2 (area 48) is a small region containing shells with *A. a. cookei* patterns. The usual form and color pattern of the shell (pl. 1, fig. 56) is more obese than the usual form in area 45, and the base is banded instead of being a solid dark color. The embryonic whorls are pale pinkish buff; postembryonic whorls white, first half of last whorl lined at the edge of the periphery with olive brown, subperipheral band white, 2 mm. wide, tinted with pale mouse gray, on the last half whorl, peripheral band warm blackish brown, subperipheral band white, 1 mm. wide, base of last whorl warm blackish brown, with a band of cream buff and a line of amber brown. Length 19.1 mm., greater diameter 13.9 mm., spire height 9.0 mm., number of whorls 6 $\frac{1}{4}$ .

The usual *cookei* base occurs on some specimens but the spire is usually lined (pl. 7, fig. 11a); postembryonic whorls pale pinkish buff spirally lined with ochraceous tawny. This shell is also the obese form. Length 19.8 mm., greater diameter 13.9 mm., spire height 10.1 mm. A rare pattern (pl. 7, fig. 11b), and an elongate shell found



on one specimen in locality 237f has the postembryonic whorls mars yellow, lined and faintly axially streaked with light buff, last whorl banded just below the edge of the periphery with pale pinkish buff, the ground below this band light buff spirally banded with mars yellow with a line of warm blackish brown; impressed sutural band russet. Length 19.0 mm., greater diameter 12.7 mm., spire height 10.7 mm. The darkest color pattern (pl. 7, fig. 11) found on only one specimen has the postembryonic whorls banded with argus brown, lined and axially streaked with light buff, last whorl just above the periphery and all below warm blackish brown. The color of the lip and columella callus is usually light vinaceous fawn.

**ACHATINELLA APEXFULVA NIGRIPICTA**, new subspecies

PLATE 1, FIGURE 55; PLATE 7, FIGURES 3-4

*Achatinella turgida simulacrum* PILSBRY and COOKE, Man. Conch., vol. 22, p. 300, pl. 56, figs. 13-13b (only), 1914.

The shell of the holotype (pl. 1, fig. 55) has the embryonic whorls white; postembryonic whorls pale pinkish buff banded with a very deep shade of diamine brown or black; impressed sutural band same black color; lip and columella callus vinaceous fawn. Length 18.2 mm., greater diameter 12.2 mm., spire height 9.3 mm., number of whorls 6.

Distribution, area 50: **Manana-Waiawa Ridge**, type locality 237b, elevation 1,450-1,500 feet, 1933; also in locality 237c, elevation 1,350-1,400 feet; 237d, elevation 1,500 feet; 237e, elevation 1,600-1,650 feet, 3 sinistral, all Meinecke-collected, 1933 (figs. 4, 4a, p. 53). Another collector of this form is Vasconcellos in 1915, for Thurston, BBM 130587-130588.

A variation (pl. 7, fig. 3) of the typical color pattern, and an elongate shell, has a lighter colored spire; postembryonic whorls pale pinkish buff spirally lined, and banded with ochraceous buff, and lined with black, last whorl at and below the periphery black with a band of pale pinkish buff just below the periphery. Length 18.8 mm., greater diameter 12.3 mm., spire height 10.5 mm. A lined pattern (pl. 7, fig. 3a) has the embryonic whorls black or a deep shade of diamine brown, lined with light buff. The color pattern (pl. 7, fig. 3b) may be solid black or a deep shade of diamine brown, which looks like a form of *A. a. apexfulva*; the last half of the first postembryonic whorl is lined with white. A rare pattern (pl. 7, fig. 3c) on one or two shells has the postembryonic whorls white spirally lined with tawny and black, banded below the periphery with black; impressed sutural band tawny. This shell also shows the usual form



of a dextral. Length 18.2 mm., greater diameter 12.5 mm., spire height 9.3 mm. One white specimen (pl. 7, fig. 3*d*) has the impressed sutural band edged with vinaceous cinnamon; last whorl below the periphery lined with chocolate. Another light color pattern (pl. 7, fig. 4) has the postembryonic whorls light buff spirally lined with black.

**ACHATINELLA APEXFULVA NIGRIPICTA var. 1**

PLATE 1, FIGURE 48; PLATE 7, FIGURES 1-2*g*

*Achatinella turgida perplexa* PILSBRY and COOKE, Man. Conch., vol. 22, p. 296, pl. 56, figs. 5*e*, 5*f* (only), 1914.

Area 44: **Waimano-Manana Ridge**, locality 223, elevation 1,250-1,300 feet, a few dextral juvenile shells, Meinecke, 1933 (figs. 4, 4*a*, p. 53). A few specimens are found in locality 225 mixed with typical *A. a. cookei* forms so that probably area 44 extends as far as this locality. Other collectors of this form are Wilder, BBM 10449-10450, Cooke, BBM 72700-72722, and J. S. Emerson, BBM 10717-10718. Their lots are usually mixed with forms from the lower region of area 40 and have been separated out from the lots of *A. a. perplexa*. The shells of area 44 are so close to *A. a. nigripicta* in form and color pattern that they can easily be confused with them. This form of *A. a. nigripicta* var. 1 usually has a more yellow ground color and no white color patterns. The placing of the bands on the shells also differs. *A. a. nigripicta* occurs opposite area 45 of *A. a. cookei* and not area 44 as one would suppose. All this region needs to be re-collected very carefully to note whether all areas have been accurately plotted.

The localized Meinecke material from area 223 is very scanty so that form and color-pattern range is not determinable. The shell may be dextral or sinistral. The embryonic whorls (pl. 1, fig. 48) are white; last two postembryonic whorls and a half pale pinkish buff spirally banded with a dark shade of diamine brown and faintly axially streaked on the last whorl above the periphery with grayish olive; lip not formed; columella callus light vinaceous fawn. A lighter color pattern (pl. 7, fig. 1) is pale pinkish buff on the postembryonic whorls, spirally lined with sayal brown, and with warm sepia on the penultimate, last whorl lined with warm buff above the periphery, warm sepia at the periphery, below the periphery, subperipheral band pale pinkish buff, a line of warm sepia and a band of cream buff about the base. A dark color pattern and a sinistral (pl. 7, fig. 1*a*), has the embryonic whorls white; first postembryonic whorl

white, banded and lined with ochraceous tawny, penultimate and last whorl above the periphery, upper half pale pinkish buff axially streaked and spirally lined with ochraceous tawny, lower half a deep shade of diamine brown or black, and banded about the base with ochraceous tawny.

In the J. S. Emerson collection there is a large series of these shells, with some *A. a. perplexa* specimens mixed from area 40. They are made up of yellow and reddish-brown patterns. The usual form and color pattern on 30 percent of the dextrals (pl. 7, fig. 2), has the embryonic whorls white; postembryonic whorls warm buff, spirally lined on the penultimate with verona brown, last whorl banded and lined with verona brown and snuff brown, peripheral band pale pinkish buff; lip and columella callus shell pink. Length 18.5 mm., greater diameter 12.7 mm., spire height 10.0 mm. The color pattern may be lighter (pl. 7, fig. 2a), postembryonic whorls warm buff, lined with ochraceous tawny; upper edge of impressed sutural band russet, lower half warm buff; base lined with warm sepia. This yellow form may be lined and banded on the last two whorls with diamine brown over a warm buff ground (pl. 7, fig. 2b). A variant of this pattern has a white peripheral band on the last whorl between the two diamine brown bands. Figure 2b shows an extreme obese dextral. Length 18.6 mm., greater diameter 14.0 mm., spire height 9.0 mm.

The reddish-brown pattern (pl. 7, fig. 2c) may be solid liver brown on the last two and a half whorls, first half postembryonic whorl ochraceous tawny and looks like a form of typical *A. a. apexfulva*. The form and usual color pattern of a sinistral shell (pl. 7, fig. 2d), has the last two whorls and a half liver brown, with a band of pale pinkish buff at the periphery on the first half of the last whorl, and a band or line of warm buff above the periphery on the last half of the last whorl. Length 19.8 mm., greater diameter 13.6 mm., spire height 10.4 mm. The shell may be narrower and more banded (pl. 7, fig. 2e). Length 19.2 mm., greater diameter 12.3 mm., spire height 10.1 mm. The first postembryonic whorl is light buff, last two whorls a dark shade of diamine brown banded on the penultimate with light buff, last whorl at and below the periphery banded with white. An extremely lined form (pl. 7, fig. 2f) has the first half of the penultimate whorl light buff spirally lined with ochraceous tawny, last whorl and a half light buff, spirally lined above the periphery with bone brown, base solid bone brown; impressed sutural band amber brown. A rare pattern (pl. 7, fig. 2g) is diamine brown, lined with pale gull gray.

**ACHATINELLA APEXFULVA NIGRIPICTA var. 2**

PLATE 2, FIGURES 1, 2; PLATE 7, FIGURES 5-6a

Area 48: **Manana-Waiawa Ridge**, locality 237g, elevation 1,750-1,800 feet, 2 dextral; 237h, elevation 1,500-1,700 feet, Meinecke, 1933.

Area 48A: **Manana-Waiawa Ridge**, locality 238a, elevation 1,750-1,900 feet; 238b elevation 1,800-1,850 feet, Meinecke, 1933 (figs. 4, 4a, p. 53).

The shells of area 48 differ from *A. a. nigripicta* in having very obese dextral shells with usually a white ground instead of a yellowish one. The usual form and color pattern of the shell (pl. 2, fig. 1) measures: Length 19.4 mm., greater diameter 13.5 mm., spire height 9.5 mm.; embryonic whorls white; postembryonic whorls white spirally banded and lined with a dark shade of diamine brown. An obese form (pl. 7, fig. 5) with a white ground and black banded postembryonic whorls measures: Length 20.3 mm., greater diameter 14.2 mm., spire height 9.8 mm.

In area 48a the color patterns are close to those of area 48. The form of the shells shows no variation from those of area 50. The darkest pattern (pl. 7, fig. 6a) has the postembryonic whorls colored a dark shade of diamine brown, last whorls banded and lined at and below the periphery with pale pinkish cinnamon. A lined color pattern (pl. 7, fig. 6) has the postembryonic whorls white tinted with light buff, lined with verona brown and black, subperipheral band white, below which are two bands of black, in the umbilical region a band of warm buff. The usual light color pattern (pl. 2, fig. 2) has the postembryonic whorls white, lined on the last two whorls just above the periphery with a line of mikado brown, at and below the periphery lined and banded with black.

**ACHATINELLA APEXFULVA SIMULACRUM** Pilsbry and Cooke

PLATE 1, FIGURE 50; PLATE 7, FIGURES 13-15a

*Achatinella turgida simulacrum* PILSBRY and COOKE, Man. Conch., vol. 22, p. 299, pl. 56, figs. 14-14d (only), 1914.

The shell figured on plate 56, figure 14a, of the Manual of Conchology is considered the lectotype of *A. a. simulacrum* and is reproduced in this paper on plate 7, figure 13. The embryonic whorls are a light shade of cartridge buff, banded on the last half embryonic whorl with a faint color of warm buff; postembryonic whorls upper half white, lower half amber brown streaked and lined with chestnut,

at the edge of the periphery of the last whorl a band of white, below the periphery a wide band of hessian brown, and a band of white lined with hessian brown, and a band of antimony yellow; impressed sutural band white; lip and columella callus vinaceous fawn. Length 18.9 mm., greater diameter 13.0 mm., spire height 9.5 mm., number of whorls 6.

Distribution, area 46: **Waimano-Manana Ridge**, locality 227a, elevation 1,550 feet, 1 sinistral 1933; 227b, elevation 1,600 feet, 3 sinistral 1933; 227c, elevation 1,700 feet, 3 sinistral 1933; 228\*, elevation 1,550-1,700 feet, 1929; 228a, elevation 1,750 feet, 1933; 229\*, elevation 1,750-1,800 feet, 1929; 229a, elevation 1,600 feet, 4 sinistral 1933, all Meinecke-collected (figs. 4, 4a, p. 53). This area also collected by H. Lenke. Lectotype, ANSP 108063. Type locality, "Waimano-Manana ridge, along the summit trail, above the locality of *A. t. cookei* (Spalding, Pilsbry, Merriam), types 108063 A.N.S." (Pilsbry and Cooke, 1914).

The type locality was probably somewhere in the region of localities 228 and 228a. The usual color pattern and form of the shell (pl. 1, fig. 50) from these localities, has the embryonic whorls pale pinkish buff shading to cream color; postembryonic whorls white with a band of ochraceous tawny just above the edge of the periphery, which band is lined with white, last whorl below the white peripheral or subperipheral band warm blackish brown with three bands of pale pinkish buff at the edge of the aperture; lip and columella callus vinaceous fawn. Length 19.6 mm., greater diameter 13.5 mm., spire height 9.5 mm., number of whorls  $6\frac{1}{4}$ .

The usual narrow form of the shell (pl. 7, fig. 14) is banded and has a color pattern resembling plate 1, figure 50, except that the last whorl is more completely banded on the base with pale pinkish buff. Length 19.4 mm., greater diameter 12.5 mm., spire height 9.6 mm.

An elongate form (pl. 7, fig. 14a) has the spire ochraceous tawny; the impressed sutural and subsutural bands white; last postembryonic whorl below the white peripheral band pale pinkish buff, banded with warm blackish brown. Length 20.7 mm., greater diameter 12.5 mm., spire height 10.2 mm. The shell may lack a wide tawny band (pl. 7, fig. 15) and be banded just above the edge of the periphery and all below with warm blackish brown, above which is a line of ochraceous tawny, remainder of the shell white. A white color pattern (pl. 7, fig. 15a) has the postembryonic whorls white, banded and lined with ochraceous tawny, last fourth whorl banded with black.

**ACHATINELLA APEXFULVA SIMULACRUM var. 1**

## PLATE 5, FIGURE 26

Area 38: **Central Waimano-North Central Waimano Ridge**, locality 212A, elevation 1,200-1,300 feet, 1 live sinistral, Meinecke, 1933; **North Central Waimano-North Waimano Ridge**, locality 215B, elevation 1,450 feet; 216B, elevation 1,450 feet; 218B, elevation 1,600-1,650 feet, 1 live sinistral, all Meinecke-collected, 1933 (figs. 4, 4a, p. 53). Since only two live shells are known from this area the range of color patterns is not known.

The shells are light color forms very similar to *A. a. simulacrum*, but differ in not having any dark-banded color patterns similar to plate 7, figure 13. A color pattern (pl. 5, fig. 26) common to the two live shells has the postembryonic whorls white spirally banded with tawny, base pale pinkish buff tinted with massicot yellow; lip not formed.

**ACHATINELLA APEXFULVA RUBIDILINEA, new subspecies**

## PLATE 1, FIGURE 51; PLATE 7, FIGURES 16-18

The shell of the holotype (pl. 1, fig. 51) has the embryonic whorls white; postembryonic whorls white profusely lined with chocolate; impressed sutural band russet; lip and columella callus light vinaceous fawn. Length 20.7 mm., greater diameter 14.0 mm., spire height 10.1 mm.

Distribution, area 47: **Manana-Waiawa Ridge**, type locality 239a, elevation 2,000-2,050 feet, Meinecke, 1933; also 239b, elevation 2,050-2,250 feet, 6 sinistral; 239c, elevation 2,100-2,300 feet, 1 sinistral, Meinecke, 1933; **North Central Waimano-North Waimano Ridge**, locality 219B, elevation 1,850-1,900 feet, 8 sinistral, Meinecke, 1933; **Waimano-Manana Ridge**, locality 220A?, Meinecke, 1929 (figs. 4, 4a, p. 53).

The form of the holotype may not be the usual shape of the shell. Only seven adult specimens are had from the type locality, so a shell that appears to be the most usual form and having the characteristic color pattern is chosen for the holotype. The color pattern on a narrow shell is lighter (pl. 7, fig. 18), entire shell white; banded on the first postembryonic whorl just above the periphery with russet, shading to mars brown, on the penultimate, last whorl lined above the periphery with cinnamon buff, below the periphery with chocolate. Length 20.2 mm., greater diameter 12.8 mm., spire height 10.2 mm.

Each locality on a different ridge has shells with color patterns showing a slightly different arrangement of bands and lines. The form



also shows a great range. All the shells of area 47, however, are reddish-brown lined or banded shells, and the ground color is usually pure white. The shells are the next race occurring above *A. a. simulacrum*.

In locality 219B the usual form of the shell (pl. 7, fig. 16) has the postembryonic whorls white tinted on the last whorl with pinkish buff, banded on the last two whorls with chocolate. Length 19.1 mm., greater diameter 13.3 mm., spire height 9.5 mm. An obese specimen (pl. 7, fig. 16a) measures: Length 20.5 mm., greater diameter 14.0 mm., spire height 10.9 mm. It has the lightest color pattern, which is white lined with chocolate and tawny.

The region of locality 220A? has dark banded forms such as plate 7, figures 17 and 17a, which are banded or lined with chocolate, or light forms which are banded and lined with kaiser brown (pl. 7, figs. 17b, 17c). The extreme obese form (pl. 7, fig. 17) measures: Length 20.6 mm., greater diameter 14.2 mm., spire height 9.7 mm. A narrow shell, figure 17b, measures: Length 19.1 mm., greater diameter 12.7 mm., spire height 10.2 mm.

**ACHATINELLA APEXFULVA CHROMATACME** Pilsbry and Cooke

PLATE 1, FIGURE 53; PLATE 6, FIGURES 20-23b

*Achatinella swiftii chromatacme* PILSBRY and COOKE, Man. Conch., vol. 22, p. 316, pl. 59, figs. 5-5b, 1914.

The subspecies *A. a. chromatacme* is closely related to *A. a. perplexa*, differing mainly in having dark-colored embryonic whorls, tan or yellowish-brown color patterns that do not occur in area 40, and the usual form having a wide light-colored band at the edge of the periphery. In rare cases the embryonic whorls may be white (pl. 6, fig. 22a), and the shell looks very much like a form of *A. a. perplexa*.

The shell of plate 59, figure 5, of the Manual of Conchology is selected by Pilsbry and myself for the lectotype of *A. a. chromatacme* and is reproduced in this paper on plate 6, figure 20. The first embryonic whorl of the lectotype is pinkish buff shading on the next whorl to cinnamon, which lightens on the upper half of the last embryonic whorl to pinkish buff; first postembryonic whorl, upper half pinkish buff lined with sayal brown, lower half sayal brown, penultimate whorl, upper half pinkish buff, lower half ecru drab axially streaked with rood's brown, last whorl above the white peripheral band vandyke brown darkening to bister, axially streaked with ecru drab, below the periphery warm sepia axially streaked with chocolate; impressed sutural band pinkish buff; lip margin army



brown; columella callus light vinaceous fawn. Length 20.1 mm., greater diameter 13.1 mm., spire height 11.1 mm., number of whorls  $6\frac{1}{4}$ .

Distribution, area 42: **Manana-Waiawa Ridge**, locality 232, elevation 1,250 feet, 1929, 3 sinistral 1933; 233, elevation 1,350 feet, 1 dextral, 6 sinistral 1929; 234\*, elevation 1,150-1,250 feet, 1929; 235\*, elevation 1,150-1,250 feet, 1929; 236\*, elevation 1,050-1,150 feet, 1929, all collected by Meinecke (figs. 4, 4a, p. 53). Lectotype, ANSP 108804, collected in **Waiawa** by Kuhns for Thaanum. Meinecke did a great deal of collecting with Kuhns and is familiar with Kuhn's localities. One or several of the above lots surely represents a series from the type locality. Meinecke, BBM 121835-121836, also reports this form from locality 230B?, elevation 1,000-1,150 feet, on the North-South Waiawa Ridge, 1929, but I am inclined to believe that the locality is wrongly plotted because of the wide difference between the color pattern of the shells of 230B\* and the adjacent localities of 231B\* and 232B\*.

The exact region of the type locality is not known to me, so I have selected locality 235 for a typical one, and shall describe the color and size variation of the shells from that place. In the usual form of the shell (pl. 6, fig. 21) and a color pattern occurring on 53 percent of the shells, the embryonic whorls shade from pale pinkish buff to tawny, last embryonic whorl banded at the suture with white; on the first postembryonic whorl and a half the impressed sutural band shades from mikado brown to cinnamon, subsutural band extending to about the middle of the whorl above the periphery, shades from cinnamon buff to cinnamon, remainder of the whorl drab axially streaked with cinnamon, last whorl and a half, impressed sutural and narrow subsutural bands cinnamon, remainder of the whorl pinkish buff closely axially streaked and finely spirally lined with drab, so that the color looks at first glance to be solid drab, at the periphery a line and a band of pale pinkish buff; lip and columella callus light vinaceous fawn. Length 19.5 mm., greater diameter 13.2 mm., spire height 10.5 mm. A narrow shell (pl. 6, fig. 21a) shows the darkest color form of the brownish or tan color patterns; the postembryonic whorls shade from walnut brown to burnt umber axially streaked with light buff; impressed sutural band light buff. Length 19.7 mm., greater diameter 12.7 mm., spire height 11.0 mm.

Forty-seven percent of the live shells in locality 235 have a gray color pattern (pl. 6, fig. 21b); the embryonic whorls shade from pale pinkish buff to russet; first postembryonic whorl shades from sayal

brown to verona brown, penultimate whorl benzo brown axially streaked with pale drab gray, last whorl drab axially streaked with pale drab gray; impressed sutural and subsutural bands white; lip and columella callus light vinaceous fawn. Length 19.1 mm., greater diameter 13.7 mm., spire height 10.0 mm. The gray pattern may be lighter (pl. 6, fig. 21*c*); postembryonic whorls white, banded on the last whorl and a half above the periphery with benzo brown, pale drab gray, and on the last fourth whorl natal brown, which bands are axially streaked with white, last whorl below the white peripheral band natal brown, axially streaked with drab and drab gray, in the umbilical region a patch of white.

Below locality 235, in localities 232, 233, 234, the brown pattern is more prevalent, and usually of a lighter color than the usual brown color pattern in locality 235. Gray color patterns are rare in these lower localities, occurring on one or two specimens in each lot; dextrals are also unusual. In the usual form and color pattern (pl. 1, fig. 53), the embryonic whorls shade from pale pinkish buff to light buff to pale pinkish buff; postembryonic whorls shade from light buff to warm buff, spirally lined with white, banded at the periphery with a line of snuff brown, and a band of white, base banded with saccardo's umber and pale pinkish buff; lip and columella callus light vinaceous fawn. Length 19.3 mm., greater diameter 12.5 mm., spire height 10.6 mm. The usual obese form (pl. 6, fig. 23) measures: Length 19.7 mm., greater diameter 13.0 mm., spire height 11.1 mm.; postembryonic whorls ochraceous tawny, base saccardo's umber tinted with ochraceous tawny. An elongate specimen (pl. 6, fig. 23*a*) measures: Length 19.4 mm., greater diameter 12.2 mm., spire height 11.5 mm.; postembryonic whorls light ochraceous buff with a central band of light brownish olive, last whorl banded above and below the cartridge buff peripheral band with light brownish olive. A rare purplish pattern (pl. 6, fig. 23*b*) has the last two whorls dark vinaceous brown, axially streaked with white, peripheral band on last whorl white; sutural and subsutural bands white.

Another common pattern in area 42 is a streaked form (pl. 6, fig. 22); the postembryonic whorls, below the subsutural and impressed sutural bands of light buff, are snuff brown axially streaked with light buff, peripheral band on last whorl pale pinkish cinnamon. The lightest color pattern (pl. 6, fig. 22*a*), and an unusual specimen in that the embryonic whorls are pale pinkish buff and not darker, has the postembryonic whorls white, last whorl lined at the edge of the periphery with a faint line of sayal brown, banded below the periphery with hair brown bands which are streaked with white.

## ACHATINELLA APEXFULVA CHROMATACME var. 1

PLATE 1, FIGURE 52; PLATE 6, FIGURES 24-24f

*Achatinella swiftii* NEWCOMB, Pilsbry and Cooke, Man. Conch., vol. 22, p. 315, pl. 59, figs. 4b, 4c (only), 1914. (While these two shells are not typically *A. a. chromatacme* var. 1, they are very close to it in color pattern.)

Area 41: **Manana-Waiawa Ridge**, locality 230\*, elevation 1,050-1,150 feet, 5 sinistral, 1929; 231\*, elevation 1,000-1,100 feet; 230A\*, elevation 1,050-1,100 feet, 3 dextral, 1 sinistral 1929; 231A\*, elevation 750-800 feet, 12 dextral 1929; 232A, elevation 550-600 feet, 1 dextral, 2 sinistral 1933, all Meinecke-collected (figs. 4, 4a, p. 53).

The shells of area 41 can easily be confused with the shells of area 40 because the embryonic whorls may be white and the color pattern similar to *A. a. perplexa*. They have been considered a variety of *A. a. chromatacme* because some of the shells have dark embryonic whorls and the range of color patterns is closer to *A. a. chromatacme* than to *A. a. perplexa*. The form is characterized by most of the patterns being spirally lined with white.

The usual form (pl. 1, fig. 52) has the first embryonic whorl pale pinkish buff, next whorl pinkish buff, last half embryonic whorl pinkish cinnamon with a central line of cinnamon; first postembryonic whorl pale pinkish buff lined with cinnamon, penultimate whorl benzo brown lined with pale pinkish buff, last whorl hair brown lined with white; impressed sutural band white, tinted pinkish buff; lip and columella callus light vinaceous fawn. Length 18.7 mm., greater diameter 12.2 mm., spire height 9.5 mm. The color pattern may be less lined (pl. 6, fig. 24) and look like *A. a. chromatacme*, first embryonic whorl and a half pale pinkish buff shading to tawny on the last embryonic whorl; postembryonic whorls pinkish buff, first postembryonic whorl axially streaked with cinnamon drab, and lined with the ground color, last two whorls lined and streaked with hair brown.

The dominant color pattern on 25 percent of the shells is a white lined pattern (pl. 6, fig. 24a); the postembryonic whorls white, first two faintly lined with mikado brown, last whorl a line of cinnamon above the periphery, at and below the periphery lined with sepia. The bands and lines may be axially streaked with white (pl. 6, fig. 24b); the shell is entirely white spirally lined with light drab, below the periphery of the last whorl a band of hair brown.

Lined brownish forms also occur. The lightest brown pattern (pl. 6, fig. 24c) has the first postembryonic whorl ochraceous tawny, with a central line of pale pinkish buff, on the penultimate and last

whorl above the periphery sutural and subsutural bands ochraceous tawny, below which is a thin band of pale pinkish buff, remainder of the whorl ochraceous tawny streaked with snuff brown, last whorl below the periphery pale pinkish buff, spirally lined with snuff brown. This specimen also shows an obese shell; length 19.1 mm., greater diameter 12.8 mm., spire height 10.1 mm. A narrow shell and dark brown color pattern (pl. 6, fig. 24*d*) has the penultimate whorl burnt umber finely lined and streaked with tilleul buff, last whorl bister axially streaked and spirally lined with snuff brown, and lined with pale pinkish buff. Length 18.6 mm., greater diameter 11.7 mm., spire height 10.3 mm.

Plate 6, figure 24*e* is a light gray pattern and obese form of a dextral shell; the postembryonic whorls pale pinkish cinnamon, the lower half of the first half postembryonic whorl dotted with cinnamon, penultimate whorl banded on the lower half of the whorl with a band of light drab shading to benzo brown axially streaked with pale pinkish buff, last whorl light drab gray with a wide sutural and subsutural band of pale pinkish buff, and a white peripheral band. Plate 6, figure 24*f*, is a narrow dextral with a color pattern similar to figure 24*d*, only the impressed sutural band is tawny.

**ACHATINELLA APEXFULVA CHROMATACME var. 2**

PLATE 1, FIGURE 54; PLATE 8, FIGURES 16, 16*a*

Area 43: **Manana-Waiawa Ridge**, locality 237\*, elevation 1,100-1,200 feet, 1929; 237*a*, elevation 1,400-1,450 feet, 1933; 237*ba*, elevation 1,300-1,400 feet, 1933, all Meinecke-collected (figs. 4, 4*a*, p. 53).

This race is of interest because it occurs between *chromatacme* and *nigripicta*. The shells are definitely more lined and have more white color pattern than *chromatacme* and one would suppose they were intermediate between a white-lined race and *A. a. chromatacme*. But above area 43 the shells have mostly a yellowish ground and are banded with warm blackish brown or liver brown. The color patterns in area 43 are so close to *A. a. chromatacme* that I think it inadvisable to separate them, although the embryonic whorls are usually light colored similar to *A. a. perplexa*.

In the usual form (pl. 8, fig. 16) the embryonic whorls shade from pale pinkish buff to light buff; postembryonic whorls pale pinkish buff spirally lined and axially streaked with light buff, last whorl and a half just above and all below the periphery warm sepia axially streaked and spirally lined with warm buff; lip and columella callus light brownish vinaceous. Length 19.1 mm., greater diameter 12.8 mm., spire height 10.4 mm.



The usual color pattern and obese form of the shell is shown on plate 1, figure 54, postembryonic whorls white; impressed sutural band on the first postembryonic whorl light pinkish cinnamon, on the remaining whorls the pinkish cinnamon color is confined to the upper edge of the band and fades out on the last whorl; last whorl banded above the periphery with hair brown, below the periphery hair brown streaked with white and lined with natal brown. Length 17.6 mm., greater diameter 13.7 mm., spire height 8.6 mm. The embryonic whorls may be darker and the postembryonic whorls lighter (pl. 8, fig. 16a); embryonic whorls pale pinkish buff shading to ochraceous buff, banded at the suture on the last embryonic whorl with sayal brown; first postembryonic whorl snuff brown lined with white, penultimate whorl white, banded and lined with sayal brown, last whorl white, lined with sayal brown and banded below the periphery with warm sepia; impressed sutural band verona brown fading out to sayal brown on the last half whorl where it occupies only the upper edge of the sutural band.

**ACHATINELLA APEXFULVA ALBIPRAETEXTA, new subspecies**

PLATE 2, FIGURE 3; PLATE 8, FIGURES 18-21

The shell is closely related to *A. a. chromatacme*, but differs in the gray banding of the postembryonic whorls, and by having white embryonic whorls. The embryonic whorls of the holotype (pl. 2, fig. 3) are white; first postembryonic whorl white, lined with russet; on the last two whorls the impressed sutural and wide subsutural bands are white, except on the last half whorl, where the lower edge of the sutural band is edged with a line of wood brown; the remainder of the shell shades from brownish drab on the first half of the penultimate to drab gray axially darkened by streaks of light drab on the remaining whorls; lip vinaceous fawn. Length 18.0 mm., greater diameter 12.5 mm., spire height 9.3 mm., number of whorls  $6\frac{1}{2}$ .

Distribution, area 63?: **North-South Waiawa Ridge**, type locality 231B\*, elevation 1,000-1,100 feet, 1929; also locality 232B\*, elevation 750-850 feet, Meinecke, 1929. The Meinecke localities were plotted in 1933 and may be plotted too low and should be checked. Also collected in **Waiawa** by Thurston, BBM 130590.

Area 64: **South Waiawa Stream**, locality 237A-1\*, elevation 750-850 feet, 3 sinistral, H. Lemke, 1932; on a spur ridge of the **North-South Waiawa Ridge**, locality 233B-1\*, elevation 1,350-1,400 feet, H. Lemke and H. Lemke, Jr., 1932. Area 63? is possibly wrongly plotted and perhaps should be placed higher or nearer area 64 (figs. 4, 4a, p. 53).



The narrow form of the shell (pl. 8, fig. 19) measures: Length 18.4 mm., greater diameter 10.8 mm., spire height 10.2 mm.; the color pattern is similar to plate 2, figure 3. An obese shell (pl. 8, fig. 20) from locality 232B exhibits the tan color pattern, which occurs on 22 percent of the shells in the type locality; the embryonic whorls are white; postembryonic whorls ochraceous buff, last half of the penultimate and last whorl just above the periphery and below the periphery mouse gray axially streaked with ochraceous buff; impressed sutural band the color of the ground except on the first post-embryonic whorl, where it is tawny. Length 19.0 mm., greater diameter 13.0 mm., spire height 10.1 mm. Two specimens of this tan color pattern were found to have the entire sutural band russet.

A dextral shell from the Thurston collection is shown on plate 8, figure 21. The color pattern is similar to plate 2, figure 3.

In locality 233B-1\*, 48 percent of the 13 dextral shells have a gray pattern similar to typical *A. a. albipraetexta*, except that the post-embryonic whorls are not banded with gray. One of these (pl. 8, fig. 18) has the embryonic whorls cartridge buff; first postembryonic whorl cream buff shading to white, lined on the first half of the whorl with tawny, the periphery faintly spirally banded or tinted with pale drab gray, below the periphery the color is drab or verona brown axially streaked with white, behind the edge of the lip is a band from 2 to 3 mm. wide of warm sepia. Plate 8, figure 18a, shows the tan color pattern that occurs on 52 percent of the dextral specimens, a color pattern similar to that of plate 8, figure 20.

Thirty-two percent of the shells in 233B-1\* are sinistral and differ in the range of color patterns from the dextral shells in having lined color patterns. The postembryonic whorls of the gray pattern (pl. 8, fig. 18b) are white spirally lined or tinted on the last two whorls with pale drab gray, just above or at the periphery a line of snuff brown, last whorl below the periphery spirally banded with pale drab gray, in the umbilical region banded with drab, pale pinkish buff, and cinnamon. The tan pattern (pl. 8, fig. 18c) has the postembryonic whorls white or pale pinkish buff, finely axially streaked or tinted with pinkish buff, last whorl banded at the edge of the periphery with white, below the periphery, spirally lined and axially streaked with a light shade of sayal brown.

**ACHATINELLA APEXFULVA GRISEIBASIS, new subspecies**

PLATE 2, FIGURE 6; PLATE 8, FIGURES 17, 17a

The shell is close to *A. a. lemkei* but differs in color pattern. The embryonic whorls of the holotype (pl. 2, fig. 6) are white except for

a line of chamois on the lower portion of the whorl just above the periphery. This can best be seen under a low-power microscope. First postembryonic whorl white, banded on the upper half of the whorl with tawny, remaining whorls white, last whorl below the periphery benzo brown axially streaked with pale drab gray; lip and columella callus vinaceous buff. Length 17.5 mm., greater diameter 12.1 mm., spire height 9.2 mm., number of whorls 6.

Distribution, area 65??: **East Waiawa**, "Ridge W. of Engineer's camp,  $\frac{1}{4}$  mi. mauka [toward the mountains] of the ditch trail from large koa tree down toward camp, on koa [*Acacia koa*], pua [*Osmanthus*], guava [*Psidium guajava*]," O. H. Emerson, BBM 103967, 1915; also J. S. Emerson, BBM 102248, 1915. The exact location is not known. The shells were surely found at a low elevation, because they were collected on trees that occur at a low elevation. Area 65?? may possibly be the approximate region of the type locality (fig. 4a, p. 53).

A variation of the typical pattern (pl. 8, fig. 17) is similar to *A. a. chromatacme* var. 2 (pl. 8, fig. 16a); first embryonic whorl white, tinted with army brown, next whorl white, faintly banded on the lower half of the whorl with cream buff; postembryonic whorls white, first half postembryonic whorl banded and streaked with ochraceous tawny, last whorl below the periphery banded with verona brown or snuff brown. The usual narrow form (pl. 8, fig. 17a) measures: Length 17.6 mm., greater diameter 11.4 mm., spire height 9.5 mm.; embryonic whorls white; first half postembryonic whorl tawny, finely lined with white, last half tawny, banded on the lower two-thirds of the whorl with sorghum brown, penultimate whorl white, banded on the first half of the whorl with sorghum brown, last half with only a line of sorghum brown lightening to sayal brown, last whorl above the periphery white, below the periphery verona brown, finely lined and axially streaked with pale pinkish cinnamon.

#### GROUP OF *A. A. POLYMORPHA* GULICK

##### *ACHATINELLA APEXFULVA POLYMORPHA* Gulick

###### PLATE 8, FIGURES 24-28a

*Apex polymorpha* GULICK, Proc. Zool. Soc. London, 1873, p. 81, pl. 10, fig. 5.  
*Apex neglectus* SMITH, Proc. Zool. Soc. London, 1873, p. 78, pl. 9, fig. 22.  
*Achatinella swiftii* NEWCOMB, Pilsbry and Cooke, Man. Conch., vol. 22, pp. 306, 307, 310, 315, pl. 59, figs. 4, 4a, 4d, 6 (only), 1914.

The holotype (pl. 8, fig. 27) has the first embryonic whorl white, remaining two and a half embryonic whorls upper half white, lower

half chamois; first postembryonic whorl light buff, with a central line of cinnamon buff, on the penultimate whorl, the subsutural band light pinkish cinnamon, remainder of the whorl light brownish drab, faintly spirally lined and axially streaked with pale pinkish cinnamon, last whorl subsutural band avellaneous, below which is a line of cartridge buff, suprapraperipheral band pale pinkish buff axially streaked with brownish drab, basal band same color but also spirally lined with brownish drab, peripheral band cartridge buff; lip cinnamon shading to white within; columella callus white; impressed sutural band shades from cameo brown on the first two whorls to wood brown on the first half of the last whorl to cinnamon on the last half whorl. Length 16.8 mm., greater diameter 12.3 mm., spire height 8.4 mm., number of whorls 6.

Distribution, area 66??: **Waipio**, Gulick. Gulick also reports the subspecies from Ahonui, Kalaikoa, Wahiawa. The district of Waipio includes Waikakalaua and Kipapa Gulches. The holotype of *A. a. polymorpha* surely did not come from north of Kipapa Gulch as Gulick reports, because the range of color patterns of one race does not extend over several gulches, although the same pattern may be repeated in widely separated areas. The holotype probably came from lower Kipapa or Panihakea Gulch in the district of Waiawa because it is similar to the shells existing in that region today. I have tentatively plotted the possible region of the type locality, area 66??, on fig. 5a, p. 105. Holotype, MCZ 39901.

A specimen (pl. 8, fig. 28) with a color pattern similar to the holotype has the embryonic whorls pale pinkish buff, banded on the lower half of the last embryonic whorl with light buff, on the first embryonic whorl at the edge of the suture a line of benzo brown; postembryonic whorls pale pinkish buff, first postembryonic whorls spirally lined with wood brown, last two whorls banded with drab, the bands lined and streaked with cinnamon drab and benzo brown; impressed sutural band russet shading to tawny on the last whorl; lip, outer margin cinnamon buff, inner margin and columella callus white. Length 16.4 mm., greater diameter 11.7 mm., spire height 8.8 mm.

The color pattern on a sinistral shell (pl. 8, fig. 28a) is much lighter and shows an elongate specimen; the first embryonic whorl and a half bicolored, upper half white, lower half hair brown, remaining embryonic whorls white, banded on the lower fourth of the whorl with a faint shade of cream buff; postembryonic whorls avellaneous spirally lined, banded, and streaked with white; impressed sutural band snuff brown on the first whorl lightening to light pinkish cinnamon on the last two whorls; lip not formed.

In the small series of shells in the Gulick collection in the Bishop Museum that can safely be identified as *A. a. polymorpha*, the typical pattern is a rare one and the range of color patterns is not determined. Usually, in Waiawa where forms similar or closely related to *A. a. polymorpha* occur, such as *A. a. polymorpha* var. 1, *A. a. flavitincta*, and *A. a. lemkei* var. 1, the sutural band is tan or brown. Exceptions to this rule are the shells of plate 8, figures 22*b* and 22*c*, of *A. a. lemkei*. But these two shells may belong to a race occurring at a higher elevation than *A. a. lemkei*. Since rare tan patterns occur with the usual banded patterns in area 68 and 69, which are very similar to the color patterns of the shell described as *Apex neglectus* by Smith, I believe that *neglectus* is a rare light tan color form of *A. a. polymorpha*.

There are four specimens of *Apex neglecta* in the type lot in the British Museum. One specimen marked "x" by myself is considered the lectotype, because it agrees best with Smith's original figure reproduced in this paper on plate 8, figure 24. The lectotype (pl. 8, fig. 24) has the embryonic whorls cartridge buff banded on the last embryonic whorl on the lower half of the whorl with cream buff; first two postembryonic whorls finely lined with cinnamon buff, last whorl pale olive gray axially streaked and faintly lined with light olive gray; impressed sutural band shades from hazel to carob brown on the last two whorls; subsutural band on the last whorl cinnamon buff; lip and columella callus vinaceous fawn. Length 17.2 mm., greater diameter 12.0 mm., number of whorls 6. Another shell from the type lot (pl. 8, fig. 25) has a convex spire, and a color pattern similar to the lectotype.

A dextral specimen in the Gulick collection (pl. 8, fig. 26) has the embryonic whorls white; postembryonic whorls pale pinkish buff spirally banded and lined with cinnamon or cinnamon buff above the periphery; the impressed sutural band mikado brown.

#### ACHATINELLA APEXFULVA POLYMORPHA var. 1

PLATE 8, FIGURES 29, 29*a*

Area?: Waiawa, J. S. Emerson, BBM 102247, BBM 33312.

The usual color pattern of the shell (pl. 8, fig. 29) resembles *A. a. polymorpha* except that the banding is a lighter shade of gray, and the base is white; the shape of the last whorl is rounded and the base is not flattened. Upper half of the first embryonic whorl white, lower half cream color, remaining embryonic whorls white, banded on the lower fourth of the whorl with warm buff; first half postembryonic whorl white, last half pinkish buff, first half of the penultimate



whorl pinkish buff spirally lined with light drab, last half pale mouse gray, lined and streaked with light buff, last whorl below the impressed sutural band light buff, banded or lined with drab and cinnamon buff, just above and below the white peripheral band are two bands of smoke gray, which shade to wood brown on the last half whorl, base white faintly lined with smoke gray; impressed sutural band amber brown shading to tawny on the last whorl; lip and columella callus pale vinaceous pink. Length 18.0 mm., greater diameter 12.2 mm., spire height 10.0 mm., number of whorls 6.

Five sinistrals are found in lot BBM 102247 of 23 shells. The color pattern on a few shells differs from the usual one. The post-embryonic whorls may be white or pale pinkish buff (pl. 8, fig. 29a), lined on the first and penultimate whorls with fawn color or wood brown, last whorl banded at the edge of the periphery with fawn color, banded below the periphery with benzo brown axially streaked with pale pinkish buff.

**ACHATINELLA APEXFULVA FLAVITINCTA**, new subspecies

PLATE 2, FIGURE 7; PLATE 8, FIGURES 30-30b

The form is closely related to *A. a. polymorpha* but differs in having the last whorl lined with dark lines of reddish brown. Plate 8, figure 30a, looks like Smith's *Apex neglectus* (pl. 8, fig. 24), except for the embryonic whorls and the lined last half postembryonic whorl.

The holotype (pl. 2, fig. 7) has the embryonic whorls bicolored, first embryonic whorl upper half white, lower half walnut brown, remaining embryonic whorls white; first postembryonic whorl white, penultimate whorl white with a faint line of light olive gray on the lower half of the whorl, last whorl above the periphery white, finely lined, axially streaked or tinted with chamois and banded above the edge of the periphery with olive buff, below the periphery banded or tinted with pallid mouse gray and lined with line and a band of benzo brown or fuscous; impressed sutural band army brown on the first whorl, on the penultimate avellaneous, on the last whorl ochraceous tawny; lip light vinaceous fawn. Length 17.2 mm., greater diameter 11.3 mm., spire height 9.5 mm., number of whorls 6.

Distribution, area 69: **Waiawa-Panihakea Ridge**, type locality 230G\*, elevation 1,200-1,250 feet, 1932; also 230Ga\*, elevation 1,300 feet, 2 dextral, 1 sinistral, 1932; 231G, elevation 1,350-1,400 feet, 1932, 5 dextral 1933; 232G\*, elevation 1,300-1,400 feet, 1932, all collected by Meinecke (figs. 4, 4a, p. 53).

The elongate form (pl. 8, fig. 30) and the usual lined color pattern which occurs on 28 percent of the shells measures: Length 17.3 mm.,



greater diameter 11.4 mm., spire height 9.6 mm., number of whorls 6; postembryonic whorls white, penultimate whorl banded above the periphery with light mouse gray, last whorl above the periphery light buff faintly lined with white, and a line of sayal brown on the first half of the whorl, 5 mm. behind the edge of the lip a streak or tinting of tawny down to the supraperipheral band of light grayish olive, last whorl banded at the periphery with white, below the periphery ground white colored with a band of light grayish olive, which is lined with two lines of fuscous; impressed sutural band changes from russet to avellaneous.

The obese form of the shell (pl. 8, fig. 30a) and a yellowish or light variant of the typical color pattern has the first postembryonic whorl and a half white, last postembryonic whorl and a half warm buff axially streaked and spirally lined with white below the periphery the ground is white or pale gull gray slightly tinted above the aperture, and at the beginning of the last half of the whorl with spots of warm buff, lined with warm sepia, on the last half of the whorl; impressed sutural band russet lightening to cinnamon buff on the last whorl. Length 16.2 mm., greater diameter 11.5 mm., spire height 8.1 mm.

The usual form of a sinistral (pl. 8, fig. 30b) and darker lined variation of the lined pattern measures: Length 17.8 mm., greater diameter 11.2 mm., spire height 10.1 mm.; postembryonic whorls cartridge buff, spirally lined and axially streaked on the first postembryonic whorl with cinnamon buff, penultimate and last whorls lined with bone brown, at the periphery banded with white, below the periphery the ground is white with a central band of bone brown which divides into three on the last half of the whorl; impressed sutural band tawny on the first whorl, on the remaining whorls cinnamon buff.

**ACHATINELLA APEXFULVA LEMKEI, new subspecies**

PLATE 2, FIGURE 5; PLATE 8, FIGURES 22-22c

The color pattern resembles *A. a. leucorraphe*, but differs in not having a white sutural band, and in having the spire tinted with yellow; first half embryonic whorl of the holotype (pl. 2, fig. 5) black, next half of whorl upper half white, lower half black, last two embryonic whorls upper half white, lower half chamois; first postembryonic whorl light buff, spirally lined with white, first half of the penultimate light buff axially streaked with cinnamon drab; the impressed sutural band on the first postembryonic whorl and a half tawny, on the last whorl and a half the sutural and subsutural

bands light buff, the remainder of the whorl hair brown, chaetura drab, or warm sepia, axially broken by straight and zigzag streaks of pale pinkish buff or white, edge of the periphery banded with white; lip and columella callus vinaceous fawn. Length 17.2 mm., greater diameter 12.0 mm., spire height 9.2 mm., number of whorls  $6\frac{1}{2}$ .

Distribution, area 67?: **North Waiawa Stream**, locality 230E-1-2?, approximate elevation 1,050-1,900 feet, "ridge back of tunnel-man's house," found on lehua (*Metrosideros*), Lemke, 1933, also 1932. The exact location of this race must be checked. Different lots from the general region of area 67? contain varying proportions of different color patterns which indicates slightly different localities (figs. 4, 4a, p. 53).

The darkest color pattern (pl. 8, fig. 22) has the first postembryonic whorl light buff finely axially streaked or tinted with ochraceous tawny, impressed sutural band ochraceous tawny, last two whorls bone brown, streaked with zigzag lines of light buff, sutural and subsutural bands light buff axially streaked with ochraceous tawny on the penultimate whorl, on the last whorl light buff, last whorl banded at the edge of the periphery with white; lip and columella callus light vinaceous fawn.

The usual color pattern of a dextral shell (pl. 8, fig. 22a) has the first postembryonic whorl white, tinted with pinkish buff, sutural and subsutural bands ochraceous tawny, penultimate whorl between white and pale pinkish buff tinted and streaked with cinnamon buff, sutural and subsutural bands cinnamon buff, just above the edge of the periphery a band of benzo brown, streaked with zigzag lines of white, last whorl above the white peripheral band pale cinnamon pink tinted with pinkish buff, supraperipheral band and all below the periphery natal brown spirally lined and streaked with zigzag axial lines of pallid mouse gray and white.

I have a number of lots before me collected by Lemke at different times from the region of the type locality. Lot 110, Lemke collection, has seven specimens, all except one with the typical pattern of plate 2, figure 5. In connection with lot 173, Lemke collection, Lemke states that he collected over a wider range, going up a spur ridge to the top of a larger ridge from which the spur branched. In this lot 45 percent of the shells have the typical patterns of *A. a. lemkei*; the remainder have white, gray-lined color patterns which possibly come from a locality at a higher elevation (see pl. 8, figs. 22b, 22c). Although I am calling these two shells *A. a. lemkei*, they quite possibly belong to another race occurring above *lemkei*, the two forms not being mixed except at the border of an upper and lower area.

The shell of plate 8, figure 22*b*, is white, last two postembryonic whorls tinted with cinnamon buff and spirally banded with pale drab gray deepening on the last half whorl to light drab and hair brown, the bands axially broken with white. The spire may be almost entirely white (pl. 8, fig. 22*c*), banded with drab below the periphery, which bands are broken by axial streaks of white, the last whorl above the periphery has a few faint lines of cinnamon buff.

ACHATINELLA APEXFULVA LEMKEI var. 1

PLATE 8, FIGURES 23-23*b*

Area 68?: North Waiawa Stream, general region of locality 233Ga?, approximate elevation 1,300 feet, Lemke, 1932, on lehua (*Metrosideros*), pua (*Osmanthus*), alani (*Pelea*) (figs. 4, 4*a*, p. 53).

The locality is a wide one and extends up to locality 234G on the Waiawa-Panihakea Ridge. The lots represent a mixture of two races, *A. a. lemkei* var. 1 and *A. a. lineipicta*. Color patterns similar to those found in locality 234G (*A. a. lineipicta*) are found mixed with color patterns not occurring in locality 234G. For discussion I shall take lot 113, Lemke collection, and describe only the unusual patterns which markedly differ from locality 234G, and occur on 48 percent of the shells.

The usual form (pl. 8, fig. 23) and color pattern of the shell has the embryonic whorls bicolored, first half embryonic whorl natal brown, shading to white on the upper fourth of the whorl, next half whorl upper half white, lower half pale drab gray, remaining embryonic whorls white banded with honey yellow just above the edge of the periphery; first postembryonic whorl light buff spirally lined with tawny; impressed sutural band tawny; remaining postembryonic whorls light buff finely lined and axially streaked with tawny, banded on the lower edge of the penultimate whorl with bone brown, last whorl below the periphery light buff, closely axially streaked, spirally lined and banded with bone brown; impressed sutural band on last two whorls light buff; lip and columella callus vinaceous fawn. Length 17.5 mm., greater diameter 12.1 mm., spire height 8.9 mm., number of whorls 6.

The color pattern may be darker (pl. 8, fig. 23*a*), the first half of the penultimate whorl russet axially streaked with tawny, last whorl and a half light buff almost entirely covered over by spiral lines and axial streaks of fuscous or carob brown; impressed sutural band light buff lined with tawny. An obese shell (pl. 8, fig. 23*b*), length 18.7 mm., greater diameter 13.5 mm., spire height 8.9 mm.,

number of whorls  $6\frac{1}{2}$ , has the postembryonic whorls light buff axially streaked with cinnamon buff; impressed sutural band on the first postembryonic whorl and a half tawny, on the remaining whorls the sutural band has the ground color; just below the periphery of the last whorl a band of white, the remainder of the base warm sepia axially streaked with zigzag lines of light buff, the edge of the periphery and just above banded with a band of warm sepia broken by the ground color. This color pattern is very similar to the typical *lemkei* pattern (pl. 2, fig. 5) except that the spire is yellow and not banded or streaked with gray on the first half of the penultimate whorl.

Although *A. a. lemkei* and its variety are not well localized, as far as the material at hand is concerned, they are of great importance to the addition of the knowledge of shell variation. Not only is there a possibility of finding new color patterns and races at different elevations on the long major ridges of the Koolau Range, but also on short spur ridges local races may be found at different elevations.

#### ACHATINELLA APEXFULVA LINEIPICTA, new subspecies

PLATE 2, FIGURE 8; PLATE 8, FIGURES 1-3a

*Achatinella swiftii* NEWCOMB, Pilsbry and Cooke, Man. Conch., vol. 22, p. 314, pl. 58, figs. 5-5b (only), 1914. Figure 5b matches *A. a. lemkei* var. 1 (pl. 8, fig. 23a) of area 68 which is an intermediate area between areas 67 and 70.

The shell is an intermediate lined form existing between the lower race of *A. a. flavitincta* (area 69) and the upper race of *A. a. ewaensis* var. 3 (area 52). The first embryonic whorl of the holotype (pl. 2, fig. 8) fawn color, remaining embryonic whorls upper third white, lower two-thirds cream buff darkening to chamois; first postembryonic whorl upper third banded with white, lower portion cinnamon buff on the first half of the whorl, last half pinkish buff lined with verona brown, last two whorls light buff above the periphery, lined with seal brown, last whorl below the periphery pale gull gray spirally banded with seal brown; impressed sutural band on first postembryonic whorl russet, on the remaining whorls light buff with a line of tawny at the lower edge of the band; lip and columella callus vinaceous fawn. Length 17.6 mm., greater diameter 12.3 mm., spire height 9.0 mm., number of whorls  $6\frac{1}{2}$ .

Distribution, area 70: **Waiawa-Panihakea Ridge**, type locality 232Ga, elevation 1,350-1,450 feet, 1933; 233G\*, elevation 1,350-1,450 feet, 1932; 234G, elevation 1,400-1,500 feet, 1933. All Meinicke-collected (figs. 4, 4a, p. 53).

The shell may be more obese and very lined (pl. 8, fig. 1), the first half embryonic whorl fuscous, next whorl upper half white, lower half light grayish olive fading to white on the last embryonic whorl and a half; the first postembryonic whorl and a half white, banded with mikado brown and lined with cinnamon buff, last postembryonic whorl and a half pale gull gray lined with black, above the periphery the ground is lined with cinnamon buff and tinted with pinkish buff; impressed sutural band russet up to the last whorl, where it fades to pinkish buff. Length 17.8 mm., greater diameter 12.8 mm., spire height 9.1 mm.

The spire may not be banded (pl. 8, fig. 1a), and the shell may be narrow, postembryonic whorls white shading to pale gull gray on the last two whorls, last whorl has a peripheral band of white, banded and lined below the periphery with fuscous. Length 17.4 mm., greater diameter 11.0 mm., spire height 9.9 mm.

Each locality in area 71 appears to have similar patterns to the type locality but the form and color pattern varies. A common form and color pattern (pl. 8, fig. 2), in locality 233G\* measures: Length 18.4 mm., greater diameter 13.1 mm., spire height 9.2 mm.; first postembryonic whorl light buff, axially streaked with light buff, penultimate whorl pale pinkish buff shading to pale gull gray on the last whorl, last two whorls profusely banded and lined with seal brown.

In locality 234G the usual form and color pattern (pl. 8, fig. 3) measures: Length 17.8 mm., greater diameter 12.6 mm., spire height 9.9 mm.; postembryonic whorls white darkening to pale gull gray, last whorl spirally lined with seal brown or black, the lines above the periphery broken by axial streaks of pale gull gray and the ground tinted with light buff; impressed sutural band ochraceous tawny becoming a dilute shade of ochraceous tawny on the last whorl. In this locality a dark color pattern (pl. 8, fig. 3a) is found on a single specimen; first postembryonic whorl and a half light buff axially streaked with chamois and lined with seal brown on the latter half of the whorl, last whorl and a half seal brown, spirally banded and lined with light buff or white.

**ACHATINELLA APEXFULVA LINEIPICTA var. 1**

PLATE 2, FIGURE 10; PLATE 8, FIGURES 4, 5

Area 72: **Panihakea-Kipapa Ridge**, locality 242-2\*, elevation 1,350-1,400 feet, 13 sinistral; 242-3\*, elevation 1,500-1,550 feet, 7 dextral, Russ and Welch, 1934, region of the upper portion of area



71 and area 72, or locality 241-1-242-3?, Russ, 1931, BBM 134151 (figs. 4, 4a, p. 53).

Area 72 is not very accurately plotted on a map. All of Welch's material consists of dead shells. The Russ material covers a considerable area so that areas 72 and 71 overlap. However, from the material on hand the shells appear to be intermediate between the forms found in area 71 and 70. The usual pattern (pl. 2, fig. 10) has the embryonic whorls similar to *A. a. lineipicta*; the first post-embryonic whorl white, penultimate whorl white deepening in color to pale pinkish buff on the last whorl, last two whorls lined above the periphery with hair brown and fuscous, last whorl at and below the periphery pale gull gray spirally lined and banded with olive brown and mouse gray; impressed sutural band russet becoming dilute in color on the last half whorl.

A few specimens have a gray color pattern (pl. 8, fig. 4), last two postembryonic whorls pale gull gray finely axially streaked and spirally lined with light gull gray. A single dark specimen (pl. 8, fig. 5) from locality 242-2\*, is white on the first postembryonic whorl, lightly axially streaked with raw sienna, on the penultimate whorl the subsutural band is warm buff axially streaked with sudan brown, the remainder of the whorl seal brown lined with warm buff, last whorl seal brown or black, subsutural band warm buff, lined with russet; impressed sutural band russet; lip light vinaceous fawn.

**ACHATINELLA APEXFULVA FUMOSITINCTA, new subspecies**

PLATE 2, FIGURE 9; PLATE 8, FIGURES 31, 31a; PLATE 9, FIGURE 1

*Achatinella swiftii* NEWCOMB, Pilsbry and Cooke, Man. Conch., vol. 22, p. 314, pl. 58, figs. 4, 4a (only), 1914.

The shell has a color pattern similar to *A. a. polymorpha* var. 1 (pl. 8, fig. 29) only it lacks the characteristic white peripheral bands on the last whorl, differs in shape and has a different series of color patterns which usually have a ground of smoke gray. The first embryonic whorl of the holotype (pl. 2, fig. 9) cream buff, remaining embryonic whorls cartridge buff, banded on the lower half of the whorl with chamois; first postembryonic whorl white, banded just above the periphery with tawny; impressed sutural and subsutural bands light vinaceous drab; penultimate and last whorls light grayish olive, tinted by fine axial streaks of smoke gray, last whorl banded at the periphery and about the base with smoke gray; impressed sutural band on the penultimate drab gray shading to avellaneous on the last whorl; lip and columella callus pale grayish vinaceous. Length

17.5 mm., greater diameter 12.5 mm., spire height 9.2 mm., number of whorls  $6\frac{1}{4}$ .

Distribution, area 71: **Panihakea-Kipapa Ridge**, type locality 240\*, elevation 1,300-1,350 feet, Meinecke, 1929; also locality 241-1a\*, elevation 1,350-1,400 feet, 5 sinistral; 241-1\*, elevation 1,250-1,450 feet; 241-2?, elevation 1,250-1,300 feet; 241-3\*, elevation 1,300-1,350 feet, Welch and Russ, 1934; 240-1-241-1a?, elevation 1,400-1,450 feet, Russ; 241-1?, Russ, 1934; all localities approximately correct. Also collected by Cooke, 1911, BBM 22826-22828, 22832 (figs. 4, 4a, p. 53).

The typical pattern occurs on 78 percent of the shells in the type locality. One light gray shell (pl. 8, fig. 31) was found in the lot which also shows a narrow specimen. Length 16.6 mm., greater diameter 11.2 mm., spire height 8.5 mm. The first postembryonic whorl and a half are white, last whorl and a half pale mouse gray darkening to drab gray on the last half whorl, tinted above the periphery with pinkish buff, banded with white and faintly lined with benzo brown. Two specimens had a chocolate-lined pattern (pl. 8, fig. 31a); postembryonic whorls pale smoke gray spirally lined, banded, and finely axially streaked with chocolate; impressed sutural band chestnut. The typical pattern (pl. 9, fig. 1) may be lined and may lack the pronounced peripheral light gray band on the last whorl, last half of first whorl and first half of penultimate whorl smoke gray spirally lined and axially streaked with chocolate, last whorl and a half smoke gray spirally lined with light grayish olive, last half whorl streaked with fuscous, last whorl streaked with pale smoke gray.

#### GROUP OF A. A. LEUCORRAPHE GULICK

#### ACHATINELLA APEXFULVA LEUCORRAPHE Gulick

##### PLATE 9, FIGURES 2-4

*Achatinella leucorraphe* GULICK, Proc. Zool. Soc. London, 1873, p. 79, pl. 10, fig. 2.—PILSBRY and COOKE, Man. Conch., vol. 22, p. 301, pl. 59, fig. 8 (only), 1914.

The holotype (pl. 9, fig. 2) has the embryonic whorls bicolored, first two embryonic whorls and a half, upper half white, lower half hair brown or fuscous black, last embryonic whorl and a half white; first postembryonic whorl pale drab gray axially streaked with benzo brown, penultimate whorl pale drab gray axially streaked with zigzag streaks of fuscous, first half of last whorl white axially streaked with fuscous, and three streaks of dark vinaceous drab above the columella, last half of the whorl drab gray axially streaked with hair

brown; impressed sutural band white; lip and columella callus white. Length 19.0 mm., greater diameter 12.6 mm., spire height 10.2 mm., number of whorls  $6\frac{1}{2}$ .

Distribution, area?: **Kalaikoa**, Gulick. Holotype, MCZ 39903. **South Kaukonahua, South-Central Branch Ridge**, general region of locality 260A?, elevation? (fig. 5, p. 105), probably the lower portion of the locality, Meinecke, 2 sinistral 1928. Found mixed with *A. a. tuberosus* var. 4, BBM 121952. Also collected by Wilder, **South Kaukonahua Stream**, BBM 50573, 1 dextral, found mixed with *A. a. virgatifulva*, BBM 50572, and probably comes from the region of Waikakalaua Stream.

One of the Meinecke shells (pl. 9, fig. 3) has the first embryonic whorl slightly worn and colored army brown, remaining embryonic whorls upper two-thirds white, lower third benzo brown, the benzo brown fades out on the last half embryonic whorl; first postembryonic whorl white, axially streaked with light drab, penultimate whorl pale gull gray axially streaked with fuscous, last whorl spirally lined and axially streaked with seal brown and fuscous, ground color pale mouse gray, and sometimes appears as zigzag streaks of pale mouse gray between the darker axial coloration, last half whorl drab, axially streaked with seal brown and fuscous; lip and columella callus a dilute shade of pale vinaceous fawn; impressed sutural band white, lined on the last whorl with a line of fuscous on the lower portion of the band; the shell is not quite adult. Length 17.5 mm., greater diameter 12.1 mm., spire height 9.7 mm., number of whorls  $6\frac{1}{4}$ .

The other Meinecke shell (pl. 9, fig. 3a) has a pattern similar to that of *A. a. leucorraphe* on the first half of the penultimate whorl, while the remaining whorls look like some form of *A. a. tuberosus*. This shell (pl. 9, fig. 3a) has the first half postembryonic whorl white with a line of fawn color on the lower fourth of the whorl broken by axial streaks of white, next three-fourths of the whorl pale gull gray axially streaked with natal brown, next half whorl pale gull gray lined with natal brown, the lines broken by the ground color, last whorl darkening to drab on the last half, spirally lined and axially streaked with white or pale gull gray.

The Wilder specimen (pl. 9, fig. 4) differs from typical *leucorraphe* by having the embryonic whorls banded with yellow. The first embryonic whorl natal brown, next whorl upper fourth white, lower fourth natal brown shading to drab, last embryonic whorl shading from drab to honey yellow; first two postembryonic whorls and a fourth white, tinted on the penultimate with pale gull gray, last whorl pale gull gray axially streaked with benzo brown; lip light buff, columella callus white.

**ACHATINELLA APEXFULVA VIRGATIFULVA, new subspecies**

PLATE 2, FIGURE 16; PLATE 9, FIGURES 5-5c

*Achatinella leucorraphe irwini* PILSBRY and COOKE, Man. Conch., vol. 22, p. 304, pl. 59, figs. 14-14b (only), 1914.

The shell resembles *A. a. leucorraphe*, to which it is closely related, but differs from *leucorraphe* in having a brown sutural band, the embryonic whorls lined on the last half embryonic whorl with yellow, and the usual absence of zigzag streaks on the postembryonic whorls. The holotype (pl. 2, fig. 16) has the embryonic whorls bicolored; embryonic whorls white, banded on the lower third of the first embryonic whorl with natal brown, on the next whorl the band fading to fawn color and finally honey yellow on the last half embryonic whorl; postembryonic whorls pale pinkish cinnamon, axially streaked with natal brown and drab; impressed sutural band chestnut; lip and columella callus white faintly tinted with pale vinaceous fawn. Length 18.4 mm., greater diameter 12.2 mm., spire height 9.6 mm., number of whorls  $6\frac{1}{4}$ .

Distribution, area 73: **Waikakalaua Stream**, Wilder, BBM 50572, exact location of Wilder's type locality not known; **Kipapa-Waikakalaua Ridge**, locality 250A-2, elevation 1,050-1,100 feet, 3 sinistral, Lemke, 1936; **North Kipapa Gulch, first North Branch**, locality 240D-1a\*, approximate elevation 900-1,000 feet, 2 dextral, Spalding, BBM 117384. Wilder's type locality probably came from somewhere in the region of localities 250A-2 and 240D-1a\*. Area 73 is considered the probable distribution of the race. This race occurs at higher elevations but is usually not dominant and mixed with the lighter tan form of *A. a. virgatifulva* var. 2 (figs. 5, 5a, p. 105).

In the Wilder lot the typical color pattern occurs on 58 percent of the shells. A variation of this pattern, the lightest color pattern and the obese form of the shell (pl. 9, fig. 5), has the first half postembryonic whorl white, axially streaked with cinnamon buff, the remaining postembryonic whorls pinkish buff axially streaked with natal brown, army brown, and bone brown; impressed sutural band russet shading to tawny on the last whorl; lip lilac buff. Length 17.5 mm., greater diameter 12.5 mm., spire height 9.6 mm.

An elongate specimen (pl. 9, fig. 5a) with the usual color of the darker color pattern occurring on 36 percent of the shells has the postembryonic whorls pinkish buff, heavily axially streaked with natal brown, the streaks broken by lines of pinkish buff; lip and columella callus white shading to light pinkish cinnamon at the outer edge. Length 19.2 mm., greater diameter 12.2 mm., spire height



11.0 mm. The darkest form of this darker color pattern (pl. 9, fig. 5b) is found on 5 specimens out of 26; first half postembryonic whorl cinnamon buff, lined with white, last half of the whorl russet, lined and streaked with pinkish buff, first three-fourths of the penultimate whorl chocolate, last fourth of penultimate and last whorl pinkish buff, spirally lined and heavily axially ornamented with closely set axial streaks of bone brown; impressed sutural band chestnut; lip and columella callus pale ochraceous buff.

On plate 9, figures 5c and 5d show the range of form of dextral specimens. Figure 5c has a color pattern similar to plate 9, figure 5. Length 17.7 mm., greater diameter 11.8 mm., spire height 9.8 mm., number of whorls  $6\frac{1}{4}$ . The shell of figure 5d has a color pattern occurring on 3 percent of the shells and looks like typical *A. a. leucorraphe* except for the brown sutural band; the last two and a half postembryonic whorls on this specimen have the first whorl white, and the last whorl and a half bone brown axially streaked and spirally lined with pale smoke gray or white. Length 17.3 mm., greater diameter 12.5 mm., spire height 8.8 mm., number of whorls  $5\frac{1}{2}$ .

On 3 percent of the shells the lined pattern of plate 9, figure 5e is found, the last two postembryonic whorls pale pinkish buff axially streaked with hair brown and spirally lined with fuscous, the lines broken by the ground color.

**ACHATINELLA APEXFULVA VIRGATIFULVA var. 1**

PLATE 2, FIGURE 20; PLATE 9, FIGURE 6

Area 75: **Waikakalaua-South Kaukonahua Ridge**, locality 260\*, elevation 1,000-1,100 feet, Meinecke, BBM 121939, 3 dextral, 1 sinistral, 1932. Also collected by Thurston, BBM 130725, 14 sinistral, probably from area 75 (figs. 5, 5a, p. 105).

Only six shells are known from locality 260\*. The shells have been separated out from area 73 because the axial streaks appear to be more closely set together and not as thick as in typical *A. a. virgatifulva*. But then certain specimens of the two areas resemble each other, so that I am undecided as to whether or not they are distinct subspecies.

A common color pattern from locality 260\* on a juvenile specimen (pl. 2, fig. 20) has the embryonic whorls bicolored, upper half white, lower half honey yellow shading to chamois; first postembryonic whorl pale pinkish buff spirally lined and axially streaked with verona brown, last whorl and a half pinkish buff, finely axially streaked with olive brown and bone brown.



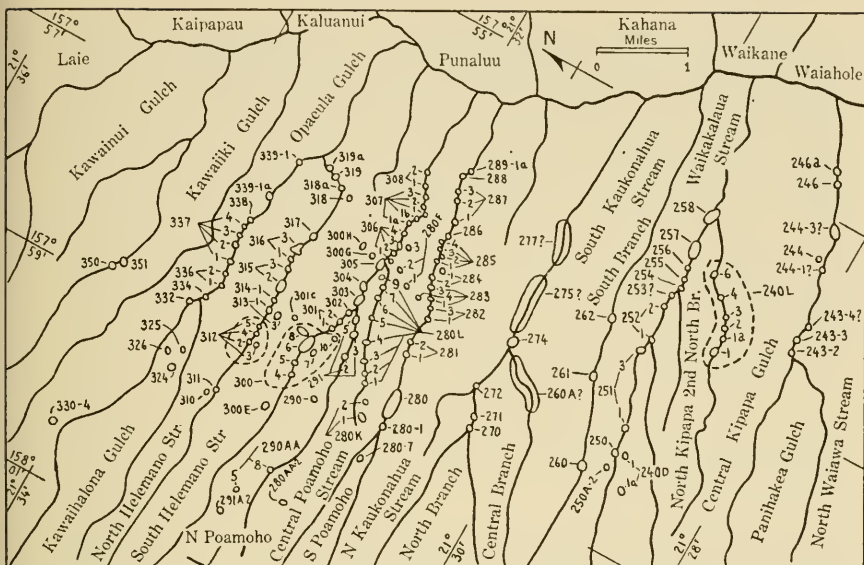


FIG. 5.—Northwest-central Oahu, leeward slope of the Koolau Range, comprising regions IIIb and most of regions III and IV (fig. 7, p. 194), showing localities of subspecies of *A. apexfulva* belonging to the groups of *A. a. polymorpha*, *A. a. irwini*, *A. a. leucorraphe*, *A. a. lilacea*, *A. a. apicata*, *A. a. aloha*, and *A. a. apexfulva*.

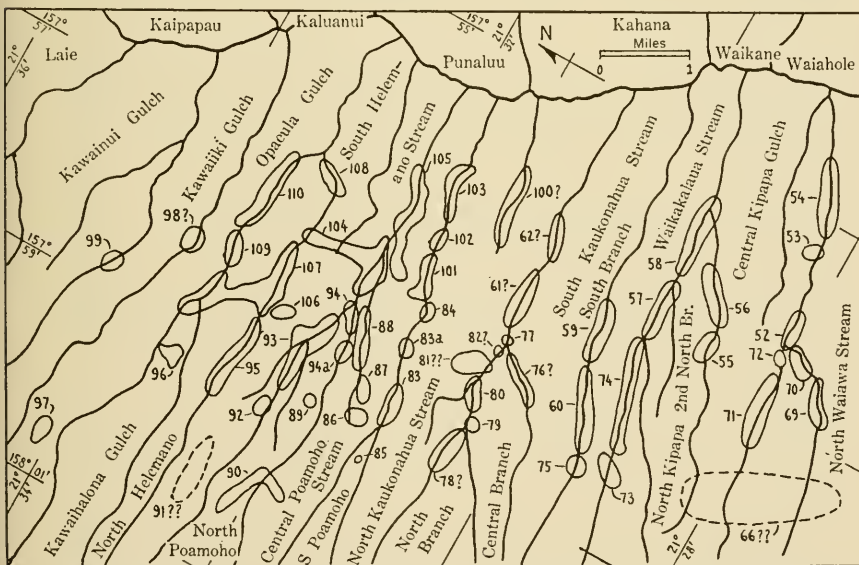


FIG. 5a.—Same as fig. 5, but showing the area occupied by different subspecies of *A. apexfulva* belonging to the groups of *A. a. polymorpha*, *A. a. irwini*, *A. a. leucorraphe*, *A. a. lilacea*, *A. a. apicata*, *A. a. aloha*, and *A. a. apexfulva*.

One of the Thurston shells (pl. 9, fig. 6) has the upper half of the first two embryonic whorls white, lower half natal brown or army brown, last embryonic whorl upper two-thirds white, lower third honey yellow; first postembryonic whorl pale pinkish buff, axially streaked with pinkish buff, first half of the penultimate whorl pale pinkish buff axially streaked with cinnamon buff, last half cinnamon buff axially streaked with mikado brown, last whorl cinnamon brown finely axially streaked with quaker drab and chocolate; impressed sutural band chestnut; lip and columella callus pale vinaceous fawn, lip outer edge light vinaceous cinnamon.

**ACHATINELLA APEXFULVA VIRGATIFULVA var. 2**

PLATE 2, FIGURE 17; PLATE 9, FIGURES 7-9

*Achatinella leucorraphe irwini* PILSBRY and COOKE, Man. Conch., vol. 22, p. 305, pl. 59, fig. 13 (only), 1914.

Area 74: **North Kipapa Gulch, first North Branch**, locality 240D-1, elevation 950-1,000 feet, 2 dextral, Lemke, 1935; **Kipapa-Waikakalaua Ridge**, locality 251-1, elevation 1,300-1,350 feet, H. Lemke, 5 dextral 1933; 250\*, elevation 1,200 feet, Meinecke, 1932; 251-1-3\*, Russ, 1931; 251-3, elevation 1,500-1,600 feet, 6 dextral, Meinecke, 1933. Also collected by Spalding and Thurston (figs. 5, 5a, p. 105).

Shells with color patterns very similar to that of *A. a. virgatifulva* var. 2 are found in lots of shells from **Waikakalaua Stream**, Wilder, BBM 50571, and **South Kaukonahua Stream**, Wilder, BBM 50573 (probably the **Waikakalaua-South Kaukonahua Ridge**).

The shell is closely related to *A. a. virgatifulva*, but differs in having a light tan streaked color pattern instead of a dark brown streaked one, and a light impressed sutural band instead of a dark brown sutural band. Specimens of *A. a. virgatifulva* are usually mixed with this form. Although the color pattern is very distinct and the form is undoubtedly a distinct one, I shall consider it a variety of *A. a. virgatifulva* until a locality is found that contains shells of *A. a. virgatifulva* var. 2 not mixed with *A. a. virgatifulva*. Most of the localities at lower elevations in areas 74, 57, 75, and 60 are wide localities and little carefully plotted material is at my disposal from this section.

The usual form (pl. 2, fig. 17) of the light color pattern has the embryonic whorls bicolored, first embryonic whorl cinnamon drab, next whorl upper half white, lower half shaded with natal brown, on the last embryonic whorl the lower band fades out and the whorl is

white; the first postembryonic whorl and a half white or pale pinkish buff, axially streaked with pale pinkish buff, last whorl and a half pale pinkish buff axially streaked with vinaceous buff, avellaneous and wood brown, and spirally lined with pale pinkish buff; impressed sutural band same as the remainder of the whorl; lip and columella callus pale vinaceous fawn, outer edge of lip pinkish buff. Length 17.7 mm., greater diameter 12.3 mm., spire height 9.4 mm., number of whorls  $6\frac{1}{4}$ .

The obese form (pl. 9, fig. 7) and light color pattern has the postembryonic whorls white, penultimate and last whorls shaded by axial streaks of a dilute color of vinaceous buff. Length 18.5 mm., greater diameter 13.1 mm., spire height 9.4 mm., number of whorls 6. An elongate specimen (pl. 9, fig. 8) has the postembryonic whorls white shading to tilleul buff on the last whorl, last two whorls axially streaked with avellaneous. Length 17.7 mm., greater diameter 11.8 mm., spire height 9.8 mm.

In the Russ lot from the region of 250-251-3\*, lined forms similar to plate 9, figure 8a, are found; the postembryonic whorls are white, penultimate faintly spirally lined or banded with cinnamon buff and sayal brown which are broken by axial streaks of white, last whorl spirally lined and banded with sayal brown and warm sepia, the lines and bands broken by axial streaks of white. This form is probably one from the upper edge of area 74 because it is similar to the form of *A. a. exvaensis* var. 6 (pl. 8, fig. 7) found in locality 251-1-2.

This light color form may be sinistral (pl. 9, fig. 9); the postembryonic whorls a yellowish hue of vinaceous buff, axially streaked with white.

#### ACHATINELLA APEXFULVA TUBERANS Gulick

##### PLATE 9, FIGURE 12

*Apex tuberans* GULICK, Proc. Zool. Soc. London, 1873, p. 81, pl. 10, fig. 3.

*Achatinella swiftii* NEWCOMB, Pilsbry and Cooke, Man. Conch., vol. 22, pp. 306, 313, 314, pl. 58, figs. 6, 9b, 11a? (only), 1914.

The holotype (pl. 9, fig. 12) in the Museum of Comparative Zoology has the embryonic whorls white, last embryonic whorl with a central band of cartridge buff; first postembryonic whorl cartridge buff, shading to tilleul buff on the last half of the whorl spirally banded on the lower fourth of the whorl with clay color darkening to benzo brown, penultimate whorl light mouse gray lined with mikado brown, benzo brown, last whorl below the white subsutural band, pale mouse gray axially streaked with light mouse gray, banded with

an upper band of mikado brown and a lower band of chocolate, peripheral band white, below the periphery white lined with mikado brown, sayal brown, and two bands of bone brown, below which is a band of sorghum brown; lip and columella callus tilleul buff; impressed sutural band shades from fawn color on the first half post-embryonic whorl to vinaceous buff on the next whorl and a half, on the last whorl white or tilleul buff. Length 19.6 mm., greater diameter 13.8 mm., spire height 10.5 mm., number of whorls 6.

Distribution, area?: **Kalaikoa**, Gulick. Also reported from Ahonui, Wahiawa, and Helemanu by Gulick. These last three localities are probably erroneous.

The typical *A. a. tuberans* pattern is not plentiful in the Gulick collection. Out of 30 specimens in the Bishop Museum marked *A. tuberans* by Gulick coming from Kalaikoa and Ahonui, only six can be said to have a pattern closely simulating the pattern of the holotype. Quite probably Gulick obtained the few specimens of *A. a. tuberans* from an entirely different place from the remainder of his material and mixed them with shells from a different region. Typical *tuberans* has not been located in recent years but the forms collected today of *A. a. tuberans* are probably closer to typical *A. a. tuberans* than most of Gulick's specimens, which undoubtedly belong to a different colony and will be dealt with under *A. a. tuberans* var. 1. The type locality of the holotype probably was somewhere at a low elevation in South Kaukonahua Stream.

**ACHATINELLA APEXFULVA TUBERANS var. 1**

PLATE 9, FIGURES 13-13c

*Achatinella swiftii* NEWCOMB, Pilsbry and Cooke, Man. Conch., vol. 22, p. 314, pl. 58, figs. 9, 9a (only), 1914.

Area?: **Kalaikoa**, Gulick. This area was probably somewhere at a low elevation in South Kaukonahua Stream.

The form is probably a race occurring near *A. a. flavida* because the ground color of so many specimens is yellow. The usual color pattern (pl. 9, fig. 13) on 45 percent of the shells has the embryonic whorls white; first postembryonic whorls white faintly axially streaked with pallid mouse gray, penultimate whorl white axially streaked and spirally lined with light mouse gray, last whorl above the periphery pale olive gray axially streaked and tinted with colonial buff and spirally lined or banded and axially streaked with natal brown, below the periphery the ground is colonial buff axially streaked and lined with dark livid brown; impressed sutural band vinaceous buff;



lip and columella callus white or a faint shade of pale vinaceous fawn. Length 18.0 mm., greater diameter 12.7 mm., spire height 9.8 mm., number of whorls  $6\frac{1}{4}$ . The usual form is not determined because of a lack of sufficient number of adult shells.

An obese shell (pl. 9, fig. 13a) and a variant of the usual pattern which does not have the lip fully developed, measures: Length 17.1 mm., greater diameter 13.5 mm., spire height 8.6 mm.; penultimate whorl white axially streaked with natal brown and spirally lined with white, last whorl chamois spirally banded and axially streaked with hay's brown above the periphery, the peripheral band is chamois axially streaked with avellaneous, below the periphery the subperipheral band is hay's brown, the remainder of the base is dark olive buff, lined and streaked with hay's brown. The light color pattern on 17 percent of the shells (pl. 9, fig. 13b) is similar to *A. a. versicolor* and has the last two whorls above the periphery white, axially streaked and spirally lined with vinaceous fawn color and army brown, on the last whorl below the periphery the ground is colonial buff spirally banded with hay's brown about the base and faintly axially streaked and spirally banded with light drab.

Thirty-eight percent of the shells have a pattern similar to that of plate 9, figure 13c, which shows a narrow shell; the first two post-embryonic whorls are pale smoke gray, spirally lined and streaked on the first postembryonic whorl with warm sepia, white, and cinnamon buff, penultimate whorl axially streaked with zigzag and straight streaks of natal brown and army brown, and spirally banded with a band of white below the suture and subsutural bands, last whorl drab gray axially streaked and lined with benzo brown and hair brown, and banded below the subsutural band and at the periphery with white, tinted with tilleul buff; the sutural and subsutural bands form a single wide band, which is natal brown axially streaked with white on the first half of the penultimate, and wood brown axially streaked with vinaceous buff on the last whorl and a half.

**ACHATINELLA APEXFULVA TUBERANS var. 2**

PLATE 2, FIGURE 21; PLATE 9, FIGURES 10-11a

*Achatinella leucorraphe irwini* PILSBRY and COOKE, Man. Conch., vol. 22, p. 304, pl. 59, fig. 9 (only), 1914.

Area 60: Waikakalaua-South Kaukonahua Ridge, locality 261\*, approximate elevation 1,450-1,529 feet, 1932; 260-261?, approximate elevation 1,100-1,529 feet, Meinecke, 1913. Locality 261 may not be very accurately plotted but is probably somewhere between localities 260 and 261 (figs. 5, 5a, p. 105).



This race is apparently an intermediate between *virgatifulva* var. 1 (area 75) and *exvaensis* var. 8 (area 59). This race usually occurs mixed with *A. a. exvaensis* var. 8, and I do not know whether it is a pure race or not. Probably the reason for the mixture is that all the collecting has been done over a wide area and the one locality that is not of wide extent may be a region where the two races overlap.

The usual color pattern (pl. 2, fig. 21) has the embryonic whorls bicolored; first half embryonic whorl hair brown, last half upper half white, lower half hair brown, next embryonic whorl and a half upper half white, lower half with two bands each covering a fourth of the whorl, the lower one benzo brown, the upper honey yellow, last half embryonic whorl upper half white, lower half chamois; first one-half postembryonic whorl white, with a line just above the edge of the periphery of chamois, next whorl white, lined with pinkish cinnamon, just above the edge of the periphery a line of verona brown, last whorl and a half white, shading to pale gull gray, spirally lined and banded with deep brownish drab; impressed sutural band white on the first postembryonic whorl and a half, on the last whorl and a half the color darkening from cartridge buff to tawny on the last whorl; lip and columella callus pale vinaceous fawn. Length 18.4 mm., greater diameter 12.2 mm., spire height 9.8 mm., number of whorls  $6\frac{1}{8}$ . The usual form is not determined because so few adult specimens of this race are at hand.

The color pattern varies. A dextral (pl. 9, fig. 10) has the postembryonic whorls white, first half of last whorl banded above the periphery with a band of avellaneous and faintly axially streaked with tilleul buff, below the periphery the axial streaks deepening to vinaceous buff, last half whorl tilleul buff axially streaked with vinaceous buff, all below the periphery and just above the periphery the base is lined, banded closely, axially streaked with fine streaks of grayish olive and benzo brown, with a dark subperipheral band of mouse gray; impressed sutural band on the last two whorls tawny; subsutural band deep quaker drab. This specimen has the light streaking of the lower race and the gray banding of the upper race.

The color pattern may be lighter (pl. 9, fig. 11); first half of penultimate pale pinkish buff, spirally lined with cinnamon buff, last whorl and a half tilleul buff, spirally lined and axially streaked with wood brown and drab.

A specimen (pl. 9, fig. 11a) is found which has a pattern very similar to the typical *tuberans* pattern (pl. 9, fig. 12). The shell is not adult; first postembryonic whorl white, spirally lined with mikado

brown, last whorl and a half white, spirally lined with mouse gray, in the umbilical region a band of pinkish buff; impressed sutural band russet.

**ACHATINELLA APEXFULVA TUBERANS** var. 3

PLATE 2, FIGURE 28; PLATE 9, FIGURES 14-15

Area 77: **North-South Kaukonahua Ridge**, locality 274, elevation 1,600-1,747 feet, Lemke, 1932, Steel, 2 dextral 1934. Also collected by Wilder, BBM 10448, and O. H. Emerson, BBM 103971, probably in the region of area 77 (figs. 5, 5a, p. 105).

This form of *A. a. tuberans* resembles typical *tuberans* very closely in color pattern. None of the specimens, however, have on the last whorl the dark bands unbroken by axial streaks that are so characteristic of typical *tuberans*. Area 77 is an intermediate one between the subspecific group of *A. a. lilacea* and *A. a. leucorraphe* because there is a mixture of both kinds of embryonic whorls in the locality. A usual color pattern (pl. 2, fig. 28) has the embryonic whorls light buff, last embryonic whorl and a half banded on the upper half of the whorl with white; penultimate and last postembryonic whorl light mouse gray spirally lined and banded with white and axially streaked with dark livid brown and hair brown; impressed sutural band ochraceous tawny with a line of bone brown on the lower half of the band, on the last whorl the upper half of the band ochraceous tawny and the bone-brown line is in the center of the band, lower half light mouse gray axially streaked with dark livid brown; below the sutural band is a line of bone brown; lip and columella callus pale ochraceous fawn. Length 21.2 mm., greater diameter 14.2 mm., spire height 11.4 mm. The usual form of the shell is not shown by figure 28. The usual length of the shell is around 19.5 mm., and has a greater diameter of 12.5 or 13.5 mm.

The color pattern may be much lighter (pl. 9, fig. 14); embryonic whorls white; first two postembryonic whorls pale pinkish cinnamon spirally lined with tilleul buff on the upper half of the penultimate whorl, lower half banded smoke gray axially streaked with pale pinkish cinnamon or white, last whorl light drab darkening to hair brown on the last half whorl, axially streaked with benzo brown, drab, and white and spirally banded and lined with white; impressed sutural band tilleul buff; lip not formed; specimen not quite adult.

The shells of area 77 seem to be an intermediate race between lower *punicea* var. 1 and the higher race of *irwini*. The Lemke lot contains shells with unicolored embryonic whorls, but one specimen

(pl. 9, fig. 14a) in the lot has embryonic whorls similar to *A. a. irwini*. The embryonic whorls are bicolored, first embryonic whorl army brown, next embryonic whorl and a half upper half white, lower half natal brown, last three-fourths embryonic whorl chamois on the lower two-thirds of the whorl, upper third white; post-embryonic whorls drab gray spirally lined with white and dusky drab, and axially streaked with white, last half whorl above the periphery almost solid dusky drab, at the edge of the periphery a band of dusky drab, above and below which is a band of white.

The Wilder and O. H. Emerson shells probably came from near area 77, the usual length of the shell is 18.5 mm., and the usual color pattern (pl. 9, fig. 15) has the last two whorls white deepening to pale gull gray on the last whorl, spirally lined above the periphery with mouse gray, the peripheral band deep mouse gray, below the white subperipheral band, the base mouse gray spirally banded with benzo brown; impressed sutural band pinkish buff. Length 18.2 mm., greater diameter 12.8 mm., spire height 9.6 mm. The Wilder specimens consisting of two shells are selected from a mixed lot containing shells from a lower locality with a different color pattern.

#### ACHATINELLA APEXFULVA TUBERANS var. 4

PLATE 2, FIGURE 23; PLATE 9, FIGURES 16-16c

*Achatinella leucorraphe irwini* PILSBRY and COOKE, Man. Conch., vol. 22, p. 305, pl. 59, figs. 16-16b (only), 1914.

Area 76?: South Kaukonahua South-Central Branch Ridge in the general region of locality 260A?, approximate elevation 1,550-1,700 feet, Meinecke, BBM 121968, 1918, BBM 121952, 1924. Other collectors of this form are Wilder, BBM 10442, O. H. Emerson, BBM 103969, J. S. Emerson. The shells of area 76 are described from the Meinecke lot, BBM 121968 (figs. 5, 5a, p. 105).

The usual color form of the shell (pl. 2, fig. 23), lot BBM 121968, has the embryonic whorls bicolored, first half whorl army brown, next whorl and a half upper half pinkish buff, lower half army brown lightening to wood brown, next embryonic whorl pinkish buff lined with white, last half embryonic whorl white; first quarter post-embryonic whorl white, next quarter whorl light buff axially streaked with warm sepia, last half of the whorl and first half of penultimate warm buff spirally lined with and streaked with warm sepia, last half of penultimate and first half of last whorl warm buff faintly lined with wood brown and a line of fawn color, last whorl banded just above the edge of the periphery with a band of sepia axially streaked

with snuff brown, below which is a band of pinkish buff, base spirally banded with sepia and snuff brown; impressed sutural band warm sepia lightening to verona brown on the last whorl; lip vinaceous fawn; columella callus white. Length 18.0 mm., greater diameter 12.2 mm., spire height 10.2 mm.

Plate 9, figure 16, is a narrow specimen and light color pattern, the last two postembryonic whorls tiller buff spirally lined with natal brown on the penultimate and hair brown and drab gray above the periphery on the last whorl, base below the white subperipheral band drab, banded with buffy brown and lined with white; impressed sutural band wood brown darkening to cinnamon on the last whorl. Length 18.0 mm., greater diameter 11.6 mm., spire height 10.2 mm.

The usual dark color form (pl. 9, fig. 16a) has the first whorl vinaceous buff, axially streaked with army brown and natal brown, last whorl and a half below the sutural band pale gull gray, lined with hay's brown, with a suprapерipheral band of hay's brown axially streaked with deep olive buff, at the edge of the periphery a band of white, below the periphery the base is avellaneous axially streaked with hay's brown and spirally lined with white; impressed sutural band verona brown. Length 17.7 mm., greater diameter 13.0 mm., spire height 9.3 mm.

A variation of the dark color pattern (pl. 9, fig. 16b) found on two specimens has the last two postembryonic whorls pale pinkish buff axially streaked and spirally lined with hair brown and chaetura drab, last whorl lined at the periphery with two lines of white, ground color of the last half whorl drab gray; impressed sutural band russet.

One specimen (pl. 9, fig. 16c) is found to have a pattern similar to that of typical *A. a. tubers*, except that the embryonic whorls are bicolored as in plate 2, figure 23; the last two whorls are pale gull gray spirally lined and banded with bone brown and natal brown, base on the last half whorl axially streaked with natal brown; impressed sutural band russet lightening to tawny on the last half whorl. One specimen similar to plate 9, figure 17c, is also found in this lot, differing only in that it has a peripheral yellow band.

**ACHATINELLA APEXFULVA TUBERANS** var. 5

PLATE 9, FIGURES 17-17e

Distribution, area?: **South Kaukonahua Stream**, Wilder, BBM 50575. This lot of shells may have come from somewhere near or along the South Kaukonahua South-Central Branch Ridge. However, no material from this ridge has been carefully localized and no accu-



rate information concerning distribution and variation has been available to me. Every lot of shells collected from the South Kaukonahua shows a different set of color patterns. Wilder's lot contained a mixture of *A. a. tuberosus* var. 4 patterns, which were mixed with decidedly smaller shells with a different range of color patterns. Therefore, the var. 4 patterns are selected out and the remaining shells are considered *tuberosus* var. 5, which may be the same or a lower race (fig. 5, p. 105). Also collected by Thurston, BBM 130737.

The usual form of the shell (pl. 9, fig. 17) has the embryonic whorls bicolored; first embryonic whorl natal brown, next whorl upper half white, lower half natal brown, last embryonic whorl and a fourth white; first half postembryonic whorl white, penultimate whorl axially streaked by straight and zigzag streaks of warm sepia and vinaceous buff, and spirally lined and banded with white, last whorl above the periphery ornamented with a band of white and a line of buffy brown and a band of vinaceous buff axially streaked with olive brown and hair brown, below the periphery the ground is white, banded with a band of bister and a band of drab axially streaked with olive brown; impressed sutural band mikado brown. Length 16.9 mm., greater diameter 11.6 mm., spire height 7.8 mm., number of whorls 6.

A narrow shell (pl. 9, fig. 17a) with lighter embryonic whorls, has a more usual color pattern which occurs on 34 percent of the shells, embryonic whorls bicolored, first embryonic whorl vinaceous buff, next whorl upper half white, lower half vinaceous buff, last embryonic whorl and a quarter white; first postembryonic whorl white spirally lined with army brown, last two whorls pale gull gray, penultimate whorl spirally lined and faintly axially streaked with fuscous, last whorl above the periphery banded with olive brown, the bands axially broken by streaks of pale gull gray, at the edge of the periphery a line of bister, below the periphery a band of pale gull gray, below this a line of bister and a band of drab axially streaked with natal brown, the remainder of the base banded with bister and drab; impressed sutural band chestnut lightening on the last half whorl to tawny. Length 16.6 mm., greater diameter 10.8 mm., spire height 9.2 mm.

The obese form (pl. 9, fig. 17b) and color pattern occurring on 28 percent of the shells has the last two postembryonic whorls white or pale gull gray spirally lined with natal brown and axially streaked with pale gull gray, just above the edge of the periphery to the edge of the periphery a band of light seal brown, base banded and



lined with natal brown; impressed sutural band vinaceous buff. Length 16.1 mm., greater diameter 11.8 mm., spire height 8.9 mm.

The lightest color pattern (pl. 9, fig. 17*c*) occurring on 31 percent of the shells has the postembryonic whorls white spirally lined on the last two whorls with light mouse gray and mouse gray, which lines are broken by axial streaks of white; impressed sutural band white, upper edge fawn color. This specimen also shows a sinistral shell. Four percent have a pattern similar to that of plate 9, figure 17*d*; postembryonic whorls white, last two whorls with a band of chocolate just above the edge of the periphery, just below the edge of the periphery a band of white, remainder of the base wood brown, lined and banded with natal brown. Two specimens in the lot of 75 shells have a color pattern resembling typical *A. a. apexfulva*. One of these (pl. 9, fig. 17*e*) has the first embryonic whorl army brown, next whorl upper two-thirds white, lower third natal brown, last embryonic whorl white; last two postembryonic whorls chocolate faintly axially streaked on the penultimate with orange cinnamon.

#### GROUP OF *A. a. IRWINI* PILSBRY AND COOKE

##### **ACHATINELLA APEXFULVA EWAENSIS, new subspecies**

PLATE 2, FIGURE 15; PLATE 7, FIGURES 23-24*a*

The shell is similar to *A. a. irwini* but differs in being smaller and having a characteristic series of reddish-brown banded color forms which differ entirely from *A. a. irwini*. The embryonic whorls of the shells of *A. a. ewaensis* and its varieties are usually banded with a deep shade of yellow such as dresden brown, chamois, or cinnamon buff. *A. a. irwini* and its varieties usually do not have the embryonic whorls banded with yellow. A few specimens of *A. a. irwini* do have the embryonic whorls banded with tints of yellow, such as cartridge buff and cream buff, but never intensely banded with yellow.

The embryonic whorls of the holotype (pl. 2, fig. 15) are bicolored, upper half white, lower half banded with dresden brown shading to buckthorn brown on the last embryonic whorl and a half; postembryonic whorls white faintly tinted with faint lines of pale gull gray, last whorl lined at and below the periphery with seal brown; lip and columella callus tinted with light brownish vinaceous. Length 17.0 mm., greater diameter 12.1 mm., spire height 8.5 mm., number of whorls 5½.

Distribution, area 56: **North-Central Kipapa Ridge**, type locality 240L-6, elevation 1,750-1,900 feet; also locality 240L-2, elevation 1,550 feet, 2 sinistral; 240L-3, elevation 1,550-1,650 feet, 1 dextral,

3 sinistral; 240L-4, elevation 1,750 feet, all Meinecke-collected, 1933 (figs. 5, 5a, p. 105).

The typical color pattern occurs on 40 percent of the shells in area 56. Thirty-three percent have a reddish-brown banded color pattern (pl. 7, fig. 24a), which has the postembryonic whorls white, lined with hay's maroon; impressed sutural band russet. Half of these reddish-brown banded shells are similar to plate 7, figure 23; last postembryonic whorl and a half white, banded just above, at, and below the periphery with hay's maroon; impressed sutural band russet. The light color form occurring on 27 percent of the shells is shown by an elongate shell (pl. 7, fig. 24); the postembryonic whorls white faintly banded with pale olive gray at the edge of the periphery, last half whorl at and below the periphery lined with black. Length 17.7 mm., greater diameter 12.0 mm., spire height 9.2 mm.

**ACHATINELLA APEXFULVA EWAENSIS var. 1**

PLATE 2, FIGURE 4; PLATE 7, FIGURES 19-20

Area 51: North-South Waiawa Ridge, locality 233Ba, elevation 1,150 feet, 1 sinistral; 233B, elevation 1,450 feet, 14 sinistral; 234B, elevation 1,500 feet; 235B, elevation 1,500-1,550 feet, 4 dextral; 236B, elevation 1,500-1,650 feet, 1 sinistral; 237B, elevation 1,700 feet, 3 dextral, 9 sinistral; 238B, elevation 1,700-1,750 feet, 1 dextral; 239B, elevation 1,700-1,750 feet, 1 dextral, 5 sinistral; North Waiawa North-South Branch Ridge, locality 230D, elevation 1,650 feet, 13 sinistral; 231D, elevation 1,700-1,750 feet, 1 sinistral; 232D, elevation 1,950-2,000 feet, 3 sinistral, all collected by Meinecke, 1933; Waiawa-Waiahole Ridge, Spalding, BBM 117388 (figs. 4, 4a, p. 53).

The color pattern of many of the forms existing in area 51 are not very strikingly different from those of the forms obtainable from area 56. The main difference is that the typical form of the shell from area 56 has the embryonic whorls more intensely banded with yellow than the shells of area 51, and a few color patterns (pl. 7, figs. 19, 19a) are not found in area 56.

The usual form and color pattern (pl. 2, fig. 4) has the first embryonic whorl pale pinkish buff, remaining embryonic whorls upper half white, lower half cream color; first half of first postembryonic whorl white, banded just above the edge of the periphery with a faint band of cream color, remaining postembryonic whorls white with a line of ochraceous buff on the last whorl and a half just above the edge of the periphery, last whorl at and below the periphery

lined and banded with seal brown; lip and columella callus pale brownish vinaceous. Length 18.4 mm., greater diameter 12.2 mm., spire height 9.0 mm.

A dextral shell (pl. 7, fig. 19) has the postembryonic whorls cartridge buff faintly tinted with lines and axial streaks of cream buff, last whorl lined and banded with seal brown; lip and columella callus vinaceous fawn.

An obese sinistral shell (pl. 7, fig. 19a), length 19.3 mm., greater diameter 13.4 mm., spire height 9.1 mm., shows a gray color pattern which is similar to the gray color patterns (pl. 8, figs. 6a, 8) found in areas 55 and 58, but not found in area 56 or other areas containing varieties of *A. a. ewaensis*. The embryonic whorls are white, banded on the lower half with chamois; postembryonic whorls white, banded on the last whorl above and below the periphery with light gull gray, and lined at the periphery on the last whorl and at the base of the last whorl with carob brown.

Four specimens in area 51 have a lined pattern (pl. 7, fig. 20) that is similar to the typical *A. a. ewaensis* color pattern (pl. 2, fig. 15) of area 56; embryonic whorls white, banded on the lower three-fourths of the whorl with warm sepia on the first whorl and shading to ochraceous tawny on the remaining embryonic whorls; postembryonic whorls white, first postembryonic whorl banded on the lower half with warm buff, last whorl and a half lined with seal brown. This shell also shows an elongate form. Length 20.1 mm., greater diameter 12.3 mm., spire height 10.7 mm.

#### ACHATINELLA APEXFULVA EWAENSIS var. 2

PLATE 2, FIGURE 12; PLATE 7, FIGURES 21-21b

Area 53: **Waiawa-Kipapa Ridge**, locality 244\*, elevation 1,500-1,700 feet, Meinecke, 1929 (figs. 5, 5a, p. 105).

The shells in area 53 differ from those of the other areas of varieties of *A. a. ewaensis* by having yellow banded color patterns (pl. 2, fig. 12; pl. 7, fig. 21). The usual form and color pattern of the shell (pl. 2, fig. 12) has the first embryonic whorl white banded on the lower fourth of the whorl with bone brown, remaining embryonic whorls upper half white, lower half cinnamon buff; postembryonic whorls white spirally banded with cinnamon buff; lip and columella callus white faintly tinted with light vinaceous fawn. Length 17.1 mm., greater diameter 11.5 mm., spire height 9.0 mm.

The color of the bands on the postembryonic whorls (pl. 7, fig. 21) may be darker, being sudan brown, and the embryonic whorls may

be larger and less blunt than those of the typical form. Eight percent of the shells are entirely white and are similar to plate 7, figure 21*a*. A dark banded form (pl. 7, fig. 21*b*) occurs on 30 percent of the shells; the postembryonic whorls shade from sudan brown axially streaked with warm buff to carob brown on the last whorl and a half, the edge of the periphery and below the periphery white, base banded and lined with carob brown.

**ACHATINELLA APEXFULVA EWAENSIS** var. 3

PLATE 2, FIGURE 11; PLATE 7, FIGURES 25, 26

Area 52: **Waiawa-Kipapa Ridge**, locality 243-2, elevation 1,500-1,550 feet, Meinecke, 1933; 243-3-4\*, elevation 1,500-1,620 feet, Meinecke, 1929, 5 dextral, 5 sinistral; 243-4\*, Welch, 1934 (figs. 5, 5*a*, p. 105).

Area 52 contains forms (pl. 2, fig. 11) similar to typical *A. a. ewaensis*, but differing in having the embryonic whorls not as markedly banded with yellow, and in having the last whorl banded with lighter reddish-brown bands. With the typical pattern are mixed color patterns (pl. 7, figs. 25, 26), which resemble the shells of area 72.

The usual form and color pattern of the shell (pl. 2, fig. 11) has the embryonic whorls bicolored, upper half or three-quarters white, lower half or fourth of the whorl banded with yellow deepening to chamois; postembryonic whorls white, last whorl below the periphery banded with chocolate; lip and columella callus pale grayish vinaceous. Length 18.7 mm., greater diameter 13.0 mm., spire height 9.3 mm., number of whorls 6 $\frac{1}{4}$ .

Out of 16 specimens from locality 243-2, 12 are dextral, 8 of which are similar to plate 2, figure 11. Three of the dextrals are similar to the shell of plate 7, figure 25, which has the postembryonic whorls white spirally lined and banded with olive buff, last whorl at the edge of the periphery banded with white, below the periphery lined with two lines of bone brown and banded with smoke gray, last half whorl lined above the white peripheral band with a line of bone brown and six lines of bone brown below the peripheral band. Length 19.0 mm., greater diameter 12.5 mm., spire height 10.2 mm.

The color pattern on three shells looks like a light form of the shells from area 71 or 72. One of these three shells (pl. 7, fig. 26) has the postembryonic whorls white, spirally lined with deep olive buff; impressed sutural band amber brown, subsutural band ochraceous tawny.

**ACHATINELLA APEXFULVA EWAENSIS** var. 4

PLATE 2, FIGURE 13; PLATE 7, FIGURES 22, 22a

Area 54: **Waiawa-Kipapa Ridge**, locality 246\*, elevation 1,800 feet, Meinecke, 1929; 246a, elevation 2,000-2,100 feet, 2 sinistral, Hosaka, 1935. Meinecke also collected a lot, BBM 118442, from the general region of locality 244 to 244-3?. But since the shells differ from those in locality 244, I shall consider the shells to have come from the region of locality 244-3?. Since the lot was collected before 1933, the shells may represent a series collected above area 53 (figs. 5, 5a, p. 105).

The yellow banded color patterns of area 53 do not occur in area 54. The usual color pattern (pl. 2, fig. 13) occurring on 77 percent of the shells in locality 246 has the embryonic whorls white, banded on the lower fourth of the whorl with a band of russet which lightens to chamois on the last half embryonic whorl; postembryonic whorls white, lined and banded on the last whorl with chocolate. Twenty-three percent have a color pattern similar to *A. a. irwini* var. 1 (pl. 8, fig. 15a) only the embryonic whorls are not like *irwini*, being banded with yellow.

The series of shells from locality 244-3? contains a mixture of patterns. A very lined form (pl. 7, fig. 22) has the first embryonic whorl upper half white, lower half verona brown, remaining embryonic whorls honey yellow on the lower three-fourths of the whorl, upper fourth white; first two postembryonic whorls shade from honey yellow to ochraceous tawny lined with white, last whorl banded and lined with carob brown. The last whorl of this shell resembles the lined pattern on the last whorl of *A. a. ewaensis* (pl. 7, fig. 24a).

The postembryonic whorls (pl. 7, fig. 22a) may be white, banded on the first two postembryonic whorls just above the edge of the periphery with buckthorn brown, last whorl banded at the edge of the periphery and below the periphery with liver brown; lip and columella callus vinaceous fawn.

**ACHATINELLA APEXFULVA EWAENSIS** var. 5

PLATE 2, FIGURE 14; PLATE 8, FIGURES 6-6b

Area 55: **North-Central Kipapa Ridge**, locality 240L-1-1a\*, elevation 1,450-1,550 feet, 1932; 240L-1, elevation 1,550 feet, 1933, Meinecke (figs. 5, 5a, p. 105).

This variety of *A. a. ewaensis* is intermediate between *A. a. ewaensis* and a lower gray race which is probably a form closely related to *A. a. virgatifulva*. The color patterns figured from area 55 are quite distinct from those of area 56, but mixed with these are a



few specimens with patterns similar to *A. a. ewaensis* patterns. Very possibly the variety is distinct enough to be considered a subspecies, but I am reluctant to so consider it until more material is available for study.

The usual color pattern (pl. 2, fig. 14) on 51 percent of the shells from locality 240L-1-1a\* has the embryonic whorls bicolored, upper third white, lower two-thirds honey yellow; postembryonic whorls white, banded just above the edge of the periphery with honey yellow on the first whorl, on the first half of the penultimate the band is cinnamon buff axially streaked with mikado brown, on the last whorl and a half the band is seal brown, below the periphery the base has a band of seal brown; lip and columella callus light vinaceous fawn. Length 17.2 mm., greater diameter 12.3 mm., spire height 8.5 mm., number of whorls  $5\frac{1}{2}$ .

Nine percent may be devoid of dark bands (pl. 8, fig. 6a), having the postembryonic whorls white, tinted with pale mouse gray; lip pale vinaceous fawn, number of whorls 6. An obese shell (pl. 8, fig. 6) shows a color pattern on 17 percent; the postembryonic whorls white tinted with gull gray, the base fuscous black axially streaked with pale smoke gray, and pale pinkish buff; lip not developed. Length 17.4 mm., greater diameter 13.5 mm., spire height 9.3 mm. The typical *ewaensis* pattern (pl. 2, fig. 15) is present on 21 percent of the shells.

One specimen is found in both lots of shells from area 55 which may be a stray shell belonging to a distinct lower race. The first embryonic whorl of one of the shells having this peculiar pattern (pl. 8, fig. 6b) is worn, the color fuscous, the next embryonic whorl upper half white, lower half pale smoke gray, last embryonic whorl white; postembryonic whorls white axially streaked with zigzag lines of bone brown, on the last whorl the white peripheral band has a line of bone brown in it at the edge of the periphery, base bone brown axially streaked with white. Length 17.2 mm., greater diameter 11.1 mm., spire height 9.5 mm.

In locality 240L-1, out of 12 live shells approximately 42 percent are similar to plate 8, figure 6a, 33 percent to plate 8, figure 6, 17 percent to plate 2, figure 14, and 8 percent to plate 8, figure 6b.

**ACHATINELLA APEXFULVA EWAENSIS var. 6**

PLATE 2, FIGURE 18; PLATE 8, FIGURES 7-7b

*Achatinella leucorraphe irwini* PILSBRY and COOKE, Man. Conch., vol. 22, pp. 304, 305, pl. 59, figs. 12, 15, 15a (only), 1914. These patterns illustrated by Pilsbry occur on the Kipapa-Waikakalaua Ridge either in area 57 or in a region including the lower part of area 57 and the upper part of area 74.

Area 57: Kipapa-Waikakalaua Ridge, locality 252-1-2?, approximate elevation 1,500-1,600 feet, 4 dextral; 253, elevation 1,650 feet, 1 dextral; 254, elevation 1,800-1,850 feet, 7 dextral; 255, elevation 1,800-1,850 feet, 2 dextral, all Meinecke-collected, 1933. In 1932 Meinecke, BBM 121935-121936, collected a series of 49 shells of this variety, which probably came from locality 252-1-2?. Another lot, BBM 121937-121938, collected by Meinecke in 1932 probably comes from locality 253?. Most of the collecting below locality 253? on this ridge is not very reliable and should be carefully checked (figs. 5, 5a, p. 105).

Although the usual form and color pattern of plate 2, figure 18, and the peculiar color patterns (pl. 8, figs. 7, 7a) of area 57, are very distinct, other patterns (pl. 8, fig. 7b) occur which are so similar to some of the color patterns (pl. 8, figs. 1, 2) of area 70 that mixed lots would be hard to separate with 100 percent accuracy. Usually the shells from area 57 are smaller than shells from area 70, and as long as the characteristic patterns of the region are present they are easy enough to separate. The Meinecke lots from 251-1-2? form the largest series available for study from area 57, and the following discussion will be based on it.

The usual form and color pattern of the shell (pl. 2, fig. 18) on 67 percent of the shells has the embryonic whorls white, banded on the lower half of the whorl with cream buff; postembryonic whorls white, last two whorls spirally lined with warm sepia; lip and columella callus light vinaceous fawn; impressed sutural band natal brown lightening to wood brown on the last half whorl. Length 17.1 mm., greater diameter 11.7 mm., spire height 9.2 mm. The spiral lines on the last whorl may be broken and the spire elongate in form (pl. 8, fig. 7); postembryonic whorls white, last whorl lined with snuff brown, the lines broken by axial streaks of white; impressed sutural band snuff brown. Length 17.0 mm., greater diameter 11.5 mm., spire height 9.2 mm. An obese shell (pl. 8, fig. 7a) has the embryonic whorls white with a single peripheral band of saccardo's umber axially streaked with white, last half whorl faintly lined with snuff brown. Length 16.4 mm., greater diameter 12.5 mm., spire height 8.2 mm.

The usual form of a sinistral and an example of the dark lined form of the shell is shown on plate 8, figure 7b, postembryonic whorls white spirally lined on the last whorl and a half with bone brown and natal brown. Length 16.6 mm., greater diameter 11.7 mm., spire height 8.8 mm. This pattern may be darker and resemble plate 8, figure 2, a shell pattern from area 70. Twenty-five percent have a white spire and a basal band similar to typical *A. a. ewaensis* (pl. 2,

fig. 15) of area 56. Two specimens have a pattern resembling plate 8, figure 6, except that the basal gray band is lighter, and two resemble plate 8, figures 7, 7a.

**ACHATINELLA APEXFULVA EWAENSIS** var. 7

PLATE 2, FIGURE 19; PLATE 8, FIGURES 8-10

Area 58: **Kipapa-Waikakalaua Ridge**, locality 256, elevation 1,750-1,800 feet; 257, elevation 1,800-1,950 feet; 258, elevation 1,900-1,950 feet, 10 dextral, Meinecke, 1933 (figs. 5, 5a, p. 105).

Lined forms similar to those occurring in area 57 (pl. 8, fig. 7b) are rare or absent in area 58. In locality 256 the ground color of the shell is white, tinted with yellow or gray; above this locality the white ground is not tinted with yellow. In the entire area the characteristic color patterns have one dark basal band or line.

The usual color pattern in area 58 (pl. 2, fig. 19) has the embryonic whorls honey yellow, upper half or three-quarters white; post-embryonic whorls white, tinted with pale gull gray above the periphery, at the periphery a band of white, tinted with cartridge buff, below the peripheral band a band of seal brown, base cartridge buff; impressed sutural band the ground color; lip and columella callus pale grayish vinaceous. Length 17.4 mm., greater diameter 12.0 mm., spire height 8.6 mm.

A variation of the typical pattern (pl. 8, fig. 8) is a two-lined pattern; postembryonic whorls above the periphery white, tinted with pale gull gray, last whorl below the periphery ivory yellow tinted with colonial buff, lined at the edge of the periphery and below the periphery by two lines of bone brown. The basal lines may be wider, becoming two basal bands. Another common pattern of this area is the white color form of plate 8, figure 6, tinted with pale gull gray. Usually the shells from area 58 have blunter embryonic whorls than the shells from areas to the south.

In the higher localities of 257 and 258 the same general plan of banding and color pattern occurs. Plate 8, figure 9, shows a dextral with a color pattern similar to that of plate 2, figure 11, except that there are two subperipheral bands instead of five. In locality 258 two very much lined specimens are found. These are the only two shells with a much banded or lined pattern in the entire area. One of these (pl. 8, fig. 10) has the first postembryonic whorl and a half white, banded on the lower half of the whorl with chamois, last whorl and a half white banded and lined with chocolate. This locality should be collected again to ascertain whether these two shells with

the lined pattern really belong to area 58 or whether they are present owing to a mixture. Shells of this pattern are more usual in areas 74 or 57.

**ACHATINELLA APEXFULVA EWAENSIS** var. 8

PLATE 2, FIGURE 22; PLATE 8, FIGURES 11-12a

Area 59: **Waikakalaua-South Kaukonahua Ridge**, general region of localities 261-262?, approximate elevation 1,450-1,529 feet, 1913; 262\*, elevation 1,450-1,500 feet, Meinecke, 15 dextral, 4 sinistral, 1932, BBM 121945-121946. Also collected by Wilder, BBM 50574, probably in the immediate vicinity of area 59 (figs. 5, 5a, p. 105).

In area 59 the shells have the first embryonic whorl and a half banded on the lower half of the whorl with brown similar to those of areas 61? and 62?, and the remaining embryonic whorls are strongly banded with yellow, resembling *A. a. ewaensis* (area 56). Some specimens in area 59 (pl. 8, fig. 12) have embryonic whorls and a color pattern very much like typical *ewaensis* (pl. 2, fig. 15) except that the bands are a lighter shade of reddish brown. The localities on this ridge are not accurately plotted and should be carefully collected again. Very probably area 59 can be divided into two areas, the upper containing shells close to *A. a. ewaensis* (pl. 2, fig. 22), the lower one having a distinct race with color patterns similar to the shells of plate 8, figures 11 and 12a, which resemble *A. a. tuberosus* var. 2.

The usual form of the shell (pl. 2, fig. 22) and common color pattern has large, flattened, bicolored embryonic whorls; first embryonic whorl white with the lower third of the whorl wood brown, next whorl upper half white, lower band wood brown, last embryonic whorl white, faintly tinted on the lower third of the first half of the whorl with a cream-buff band; postembryonic whorls white spirally banded just above the periphery on the last two whorls with tawny which shades to light grayish olive on the last half whorl, below the periphery of the last whorl a single band of hay's maroon; lip and columella callus pale grayish vinaceous. Length 18.1 mm., greater diameter 12.8 mm., spire height 8.5 mm., number of whorls 5 $\frac{3}{4}$ . The last whorl may have all manner of variations; the subperipheral and suprapерipheral bands may be made of two smaller bands or lines, or the band above the periphery may be hay's maroon as well as the lower band.

A gray color pattern (pl. 8, fig. 11) found on one or two specimens in area 59, has the first embryonic whorl white, lower third natal brown, remaining embryonic whorls banded on the lower third with



a band of wood brown shading to chamois; first two postembryonic whorls banded just above the edge of the periphery with a band of cream buff shading to pinkish cinnamon, last whorl above the periphery white, lined and banded with a band of cinnamon buff, which band is axially streaked with pale pinkish buff and mikado brown, last half whorl bone brown axially streaked with pale pinkish buff, below the periphery a band of white; impressed sutural band on the first postembryonic whorl white, on the penultimate pinkish buff shading to mikado brown on the last whorl.

In locality 262\* (BBM 121946) collected in 1932 by Meinecke, the shells are 78 percent dextral, and only 17 percent have a gray pattern similar to that of plate 8, figure 11. The common color pattern (pl. 8, fig. 12) has the embryonic whorls bicolored, upper half white, lower half honey yellow; postembryonic whorls white, last whorl banded with army brown, shape ovate. Length 18.6 mm., greater diameter 13.0 mm., spire height 9.0 mm. An elongate shell with dark bands and ochraceous tawny lines (pl. 8, fig. 12a) has a color pattern found on only one specimen; the postembryonic whorls are white, spirally lined or banded above the periphery with ochraceous tawny, last whorl banded at and below the periphery with hay's maroon. Length 19.7 mm., greater diameter 12.6 mm., spire height 10.8 mm.

**ACHATINELLA APEXFULVA IRWINI** Pilsbry and Cooke

PLATE 2, FIGURE 29; PLATE 8, FIGURES 13-14a

*Achatinella leucorraphe irwini* PILSBRY and COOKE, Man. Conch., vol. 22, pp. 302, 303, pl. 59, fig. 11a (only), 1914.

The lectotype of *A. a. irwini* selected by Pilsbry and myself is figured in the Manual of Conchology on plate 59, figure 11a, and is reproduced in this paper on plate 8, figure 13. The embryonic whorls of the lectotype are bicolored, first embryonic whorl warm sepia, remaining embryonic whorls upper half or fourth cartridge buff or white, lower portion lightens from warm sepia to cream buff on the last whorl; postembryonic whorls white, lined with one or two faint lines of ochraceous buff, last whorl lined at the edge of the periphery with a line of grayish olive, below the periphery a line of light buff, below which are three lines and two bands of warm blackish brown and a basal band of ochraceous buff, and one of warm blackish brown; impressed sutural band warm sepia, shading to bister on the penultimate and first half of the last whorl, on the last half the impressed sutural band is white, the upper edge lined with a line of sayal brown, the lower edge warm blackish brown; lip pale vinaceous fawn. Length 19.0 mm., greater diameter 12.2 mm., spire height



9.6 mm., number of whorls 6. The color pattern of the lectotype is a characteristic one of the North-South Kaukonahua Ridge.

Distribution, area 61?: **North-South Kaukonahua Ridge**, locality 275?, approximate elevation 1,650-1,810 feet, Meinecke, 1923 (figs. 5, 5a, p. 105). Also collected by Wilder, BBM 50576. Lectotype, ANSP 108778. Type locality, the "upper part of the Kaukinehua [Kaukonahua] ridge" (Pilsbry and Cooke, 1914), collected by I. Spalding.

In the Wilder collection there is a series of 22 shells, all sinistral, which probably come from the region of the type locality or the locality of the lectotype. Wilder collected with Spalding, and it is probable that the Wilder lot is from the same place. The shells in the Wilder lot have a uniform color pattern which may mean either that Wilder selected out his color patterns, or that the lot is from a localized area of fairly limited extent. I am inclined to believe it is from a small area because the shells are very similar to those obtained by Meinecke on this ridge in area 61?.

The usual form of the shell in the Wilder lot, BBM 50576 (pl. 2, fig. 29), and the color pattern on 59 percent of the shells has the embryonic whorls bicolored, first whorl cinnamon drab, next whorl upper half white, lower half cinnamon drab, last embryonic whorl white; postembryonic whorls white, lined just above or at the edge of the periphery with sayal brown, last whorl and a half spirally lined with sayal brown and cinnamon buff; lip and columella callus pale vinaceous fawn. Length 18.5 mm., greater diameter 12.3 mm., spire height 9.7 mm.

A variation of the typical pattern (pl. 8, fig. 14) found on three shells is a light pattern; postembryonic whorls white, last whorl at the edge of the periphery faintly banded with pale pinkish buff and cinnamon buff. Another characteristic color pattern (pl. 8, fig. 14a) occurring on 27 percent has the postembryonic whorls white, last whorls faintly spirally lined and banded with pale pinkish buff, last whorl lined at the edge of the periphery and banded and lined below the periphery with hay's maroon; impressed sutural band, on the first postembryonic whorl and a half russet, on the last whorl and a half light buff with a line of russet on the lower half of the band.

**ACHATINELLA APEXFULVA IRWINI var. 1**

PLATE 2, FIGURE 30; PLATE 8, FIGURES 15-15b

*Achatinella leucorraphe irwini* PILSBRY and COOKE, Man. Conch., vol. 22, pp. 302, 303, pl. 59, figs. 10, 11, 11b (only), 1914.

Area 62?: **North-South Kaukonahua Ridge**, locality 277?, elevation 1,750-1,900 feet, Meinecke, BBM 122671, 1923, BBM 121973-121974, 1918 (figs. 5, 5a, p. 105).

The usual form of the shell and the form and color pattern of the embryonic whorls are close to *A. a. irwini*. The usual color pattern of the postembryonic whorls is almost identical with the color pattern of the holotype of *A. a. ewaensis*. The two forms of *A. a. ewaensis* are separable because this form does not have a yellow band on the embryonic whorls and has a different range of color patterns.

The usual form (pl. 2, fig. 30) and color pattern on 50 percent of the sinistral shells has the embryonic whorls bicolored, first two embryonic whorls white, banded on the lower third of the whorl with fuscous; postembryonic whorls white faintly tinted with pale gull gray, last whorl banded and lined with seal brown; lip and columella callus pale grayish vinaceous. Length 18.5 mm., greater diameter 12.6 mm., spire height 9.0 mm. A variation of the usual form is a broad banded color pattern (pl. 8, fig. 15) with the same color as plate 2, figure 30. Eighteen percent of the sinistrals have a white color pattern tinted with gray similar to plate 8, figure 6a. Twelve percent may have olive buff or yellow lines similar to *A. a. irwini* mixed with the usual pattern.

The usual form of a dextral (pl. 8, fig. 15a) and color pattern on 50 percent of the dextral shells has the postembryonic whorls white, last whorl faintly lined at the edge of the periphery with pale gull gray, base lined with seal brown. Length 18.2 mm., greater diameter 12.5 mm., spire height 9.3 mm. Twenty-two percent have the banded pattern of plate 8, figure 15, 11 percent have a white pattern similar to plate 8, figure 6a. Seventeen percent have an unusual dark banded pattern (pl. 8, fig. 15b); last two postembryonic whorls dark livid brown banded with pale vinaceous fawn, the bands lined with wood brown or vinaceous buff.

The dextrals do not contain any forms with olive buff or yellow in them similar to *A. a. irwini*. For this reason I believe the dextrals probably came from a higher locality than the sinistrals and probably occur as a pure race of dextrals. The sinistrals may also occur as a pure white banded race without any olive buff or yellow lines on the shell. This section of the North-South Kaukonahua Ridge is not well known and should be carefully collected again.

#### GROUP OF *A. a. CONIFORMIS* GULICK

#### *ACHATINELLA APEXFULVA CONIFORMIS* Gulick

##### PLATE 2, FIGURE 34; PLATE 9, FIGURES 18-20a

*Apex coniformis* GULICK, Proc. Zool. Soc. London, 1873, p. 80, pl. 9, fig. 17.  
*Achatinella swiftii* NEWCOMB, Pilsbry and Cooke, Man. Conch., vol. 22, pp. 306, 308, 309, 312, pl. 58, figs. 2, 2a, 7; pl. 59, figs. 1a, 1b, 2(?); pl. 60, fig. 10a (only), 1914.

*Achatinella apexfulva apicata* (Newcomb) PFEIFFER, Pilsbry and Cooke, Man. Conch., vol. 22, pp. 325-326, 327, pl. 60, figs. 5(?), 10a, 1914.

The holotype of *A. a. coniformis* (pl. 9, fig. 18) has the first embryonic whorl and a half white, remaining embryonic whorls light buff; postembryonic whorls pinkish buff axially streaked with avellaneous, last whorl also spirally lined with avellaneous, last 6.4 mm. of the last whorl mikado brown; impressed sutural band russet; lip and columella callus pale cinnamon pink. Length 17.5 mm., greater diameter 12.7 mm., spire height 8.7 mm., number of whorls  $6\frac{1}{2}$ .

Distribution, area?: Type locality **Ahonui**, Gulick. Holotype, MCZ 39911. Also Kalaikoa, Wahiawa, Helemano, Gulick. These last three localities are undoubtedly an error because all subspecies of *A. apexfulva* found today at a low elevation in the region between South Kaukonahua Stream and Helemano Stream are highly localized. The area occupied by a single race usually covers less than a mile in extent along the top of a ridge or bottom of a gulch, and never extends over two main ridges. Gulick and Smith named a series of species such as *coniformis*, *flavida*, *versicolor*, *gulickii*, and *lilacea* which are undoubtedly distinct subspecies from highly localized localities. However, in the Gulick collection specimens of these very distinct forms are reported from a number of widely separated localities. This indicates that the Gulick collection is a mixture of shells from various localities. This may be accounted for by the fact that most of Gulick's material was obtained from natives.

The typical color pattern of *A. a. coniformis* is exceedingly rare in the Gulick collection in the Bishop Museum, only four juvenile specimens being found. The lots from Ahonui containing these specimens also include a diversity of patterns that belong to other subspecies such as *A. a. gulickii* and *A. a. lilacea*.

An elongate form of the shell with a light shade of the typical color pattern (pl. 9, fig. 19) has the embryonic whorls pale pinkish buff; postembryonic whorls a yellowish hue of avellaneous, spirally lined above the periphery with tilleul buff and fawn color; impressed sutural band mikado brown. A darker shell of the typical color pattern (pl. 9, fig. 19a), also a juvenile, has the embryonic whorls light buff darkening to pinkish buff; postembryonic whorls avellaneous spirally lined and axially streaked with cameo brown, last whorl finely axially streaked with verona brown and spirally lined with light pinkish cinnamon. A specimen that looks like a brown form of *A. a. gulickii* has the first postembryonic and penultimate whorls, above the wood brown suprapерipheral band, light drab spirally lined and finely axially streaked with white, last whorl wood brown spirally

lined with white or tilleur buff and axially streaked with benzo brown, peripheral band white; lip and columella callus light pinkish cinnamon.

Mixed with other lots of shells of various subspecies from Ahonui, Kalaikoa, and Wahiawa, a group of distinct color patterns occur which resemble *A. a. coniformis*. All shells similar to *coniformis* are markedly ornamented with fine spiral lines and weakly streaked with fine axial streaks. These forms (pl. 2, fig. 34; pl. 9, figs. 20, 20a) probably came from a single locality or from the same general area as the holotype of *A. a. coniformis*. The holotype is probably a rare color pattern of the subspecies.

In the usual form and color pattern (pl. 2, fig. 34) of *A. a. coniformis* the embryonic whorls shade from white to light buff; first three-fourths postembryonic whorl white axially streaked with brownish drab, next whorl and a fourth dark gray axially streaked and faintly spirally lined with white, last whorl light drab, shading to snuff brown on the last fourth whorl, axially streaked and spirally lined with white; impressed sutural band on the first postembryonic whorl the same as on the rest of the whorl, on the remaining whorls white; lip not completely thickened, color avellaneous; columella callus white tinted with pale vinaceous fawn. Length 17.8 mm., greater diameter 12.5 mm., spire height 9.8 mm., number of whorls  $6\frac{3}{4}$ .

The color pattern may be more brownish (pl. 9, fig. 20) and the form more elongate than the usual form; embryonic whorls white; first postembryonic whorls, up to the last whorl, tilleur buff axially streaked with pallid mouse gray, last whorl a yellowish hue of vinaceous buff spirally lined with white; impressed sutural band same as rest of whorl; lip light vinaceous fawn. Length 18.3 mm., greater diameter 11.7 mm., spire height 9.4 mm. An obese and strongly lineate form (pl. 9, fig. 20a) has the first two embryonic whorls white, last embryonic whorl cream color; first postembryonic whorl vinaceous drab, lined with white, penultimate whorl light drab spirally lined and axially streaked with white, last whorl drab spirally banded above the periphery with a band of white which is lined with four lines of drab, below the periphery ground lined and streaked with white; lip and columella callus light vinaceous fawn. Length 17.4 mm., greater diameter 13.2 mm., spire height 9.4 mm.

**ACHATINELLA APEXFULVA APEXALBA, new subspecies**

PLATE 2, FIGURE 35; PLATE 9, FIGURES 26-26d

*Achatinella swiftii* NEWCOMB, Pilsbry and Cooke, Man. Conch., vol. 22, pp. 308, 309, 312, pl. 58, figs. 1, 2b, 2c, 16; pl. 59, fig. 1 (only), 1914.

The shell is usually sinistral and resembles the form of *A. a. versicolor*, but differs from *A. a. versicolor* by lacking a white periph-



eral band and having a different range of color patterns. The shell has characteristic white embryonic whorls and contrasting dark brown postembryonic whorls. This subspecies is usually found mixed with *A. a. coniformis* in the Gulick lots although some lots of *apexalba* contain no forms of *A. a. coniformis*. I have separated *apexalba* from *coniformis* because of the fact that *apexalba* has a crisscross color pattern in which the spiral bands are broken or flecked by dark and light axial streaks somewhat resembling *A. a. versicolor*. The shell of *apexalba* has a rough, coarse, or broken pattern, whereas *coniformis* has a solid, finely axially streaked even color. A few specimens are found which might be put in either subspecies. These are probably intermediate forms between the two races.

The embryonic whorls of the holotype (pl. 2, fig. 35) are pale pinkish buff; first two postembryonic whorls light drab axially streaked with hair brown and benzo brown spirally lined with a central line of white, on the penultimate whorl a white subsutural band broken by dark axial streaks, last whorl above and just below the periphery spirally banded with light drab and drab axially streaked with snuff brown, flecked and spirally lined with white, last half whorl darkens to snuff brown, base snuff brown spirally banded with avellaneous and tilleul buff; impressed sutural band chestnut on the first two postembryonic whorls, on the last whorl impressed sutural band the ground color except the upper edge, which is fawn color; lip and columella callus pale vinaceous fawn. Length 18.5 mm., greater diameter 11.7 mm., spire height 10.0 mm., number of whorls 6 $\frac{1}{4}$ .

Distribution, area?: Type locality **Wahiawa**, Gulick. Also Kalai-koa, Ahonui, Gulick. The last two localities are probably wrong, if Wahiawa is correct.

The darkest color pattern and elongate form of the shell (pl. 9, fig. 26) measures: Length 17.9 mm., greater diameter 11.3 mm., spire height 10.8 mm.; first two postembryonic whorls drab spirally banded with fawn color and axially streaked with verona brown, last whorl saccardo's umber, banded with fawn color above the periphery, below the periphery a band of white and lines of white; impressed sutural band russet lightening in color at the extreme upper edge to tawny.

A light color pattern (pl. 9, fig. 26a) has the first postembryonic whorl benzo brown with a central white line, penultimate whorl white axially streaked with hair brown and spirally lined with a central band of white, last whorl tilleul buff, spirally lined with verona brown and axially streaked with drab, base banded with a hue between benzo



brown and hair brown; impressed sutural band warm sepia lightening to sayal brown on the last half whorl, subsutural band shades from benzo brown to hair brown and verona brown on the last half whorl.

An extreme obese specimen (pl. 9, fig. 26*b*) has the embryonic whorls white; postembryonic whorls drab axially streaked with hair brown, and on the last whorl also streaked with tilleul buff, on the last two whorls just above the edge of the periphery two lines of white broken by the axial ornamentation, base weakly lined with white; impressed sutural band russet lightening to tawny on the last half whorl. Length 17.6 mm., greater diameter 13.0 mm., spire height 9.2 mm.

A lighter gray color pattern (pl. 9, fig. 26*d*) is strongly axially streaked on the last two postembryonic whorls; penultimate whorl benzo brown, lined with pinkish buff and white and streaked with pale smoke gray, last whorl pale smoke gray lightening to pale cinnamon pink, axially streaked with light drab, spirally banded with drab below the sutural band, and lined with white above and below the periphery. The color may be a very light brownish hue (pl. 9, fig. 26*c*), penultimate whorl similar to that of figure 26*d*, last whorl avellaneous lined with white.

#### ACHATINELLA APEXFULVA VERSICOLOR Gulick

PLATE 2, FIGURE 33; PLATE 9, FIGURES 21-23

*Apex versicolor* GULICK, Proc. Zool. Soc. London, 1873, p. 80, pl. 9, fig. 18.

*Achatinella swiftii* NEWCOMB, Pilsbry and Cooke, Man. Conch., vol. 22, pp. 306, 310, pl. 58, figs. 14-14*d*, 15 (only), 1914.

The holotype (pl. 9, fig. 21) has the first embryonic whorl and a half cartridge buff, remaining embryonic whorls cream buff, lined with white; first quarter postembryonic whorl upper half pale gull gray, lower half banded and lined with chamois, remaining postembryonic whorls pale gull gray axially streaked with mouse gray on the penultimate, just above the edge of the periphery a band of bone brown or clove brown up to the last whorl, last whorl pale mouse gray axially streaked with benzo brown, banded above the pale mouse gray peripheral band, and all below, with hay's brown, streaked with pale mouse gray; impressed sutural band the ground color; lip and columella callus pale vinaceous fawn. Length 18.8 mm., greater diameter 13.0 mm., spire height 9.5 mm., number of whorls 6.

Distribution, area?: Type locality, *Ahonui*, Gulick. Also Kalaikoa, Gulick. This race probably occurred somewhere in the region of the North or South Kaukonahua Stream.

The usual form of *A. a. versicolor* (pl. 2, fig. 33) measures: Length 17.2 mm., greater diameter 11.6 mm., spire height 9.2 mm., number of whorls 6; embryonic whorls light buff, lined or banded on the last whorl with white; first half postembryonic whorl pale gull gray, spirally lined with benzo brown below the impressed sutural band of benzo brown, just above the edge of the periphery a line of sayal brown, last half of whorl pale gull gray with an axial streak of snuff brown, first half of the penultimate pale gull gray axially streaked with cinnamon buff, last whorl and a half white or faintly shaded with pallid mouse gray, axially streaked with snuff brown and the ground color, spirally banded or lined with snuff brown and bister, below the edge of the periphery a band of white, base bister axially streaked with white.

A light color pattern (pl. 9, fig. 23) has the postembryonic whorls white or faintly shaded with pallid mouse gray, first postembryonic whorl and a half has a subsutural line of mouse gray, last postembryonic whorl and a half spirally lined and axially streaked with mikado brown and sayal brown, subperipheral band white, base banded with warm sepia and a line of white. A rare pattern (pl. 9, fig. 22) has the last postembryonic whorl above the periphery white shaded with pale gull gray, with a patch or streak of snuff brown above the aperture and on the last half of the whorl, the band at the edge of the periphery, and all below the white subperipheral band, drab axially streaked with benzo brown.

#### ACHATINELLA APEXFULVA VERSICOLOR var. 1

##### PLATE 9, FIGURES 24-25b

*Achatinella swiftii* NEWCOMB, Pilsbry and Cooke, Man. Conch., vol. 22, p. 314, pl. 58, figs. 3, 3a, 11; pl. 59, fig. 2, 1914.

*Achatinella apexfulva apicata* (Newcomb) PFEIFFER, Pilsbry and Cooke, Man. Conch., vol. 22, p. 325, pl. 60, fig. 5a (only), 1914.

Area 78?: Somewhere at a low elevation below area 79 probably in area 78? (figs. 5, 5a, p. 105), on the **North-South Kaukonahua Ridge**, Thurston, BBM 130693-130694, Judd, BBM 110053-110054. Also collected by Gulick and mixed with subspecies of *A. apexfulva* from Kalaikoa and Ahonui.

*A. a. versicolor* var. 1 is a race of bluish-gray shells with certain color patterns that resemble those of *A. a. versicolor*, but most of its patterns are quite distinct.

A characteristic color pattern (pl. 9, fig. 25) has the postembryonic whorls white, banded just above the periphery and on the last whorl

above and below the periphery with light mouse gray lined with white; impressed sutural band mouse gray with a line of verona brown along the upper edge; lip and columella callus pale vinaceous fawn. Length 19.0 mm., greater diameter 11.7 mm., spire height 10.0 mm.

A dark color pattern and an elongate shell (pl. 9, fig. 25*a*) measures: Length 19.4 mm., greater diameter 12.1 mm., spire height 11.0 mm. The postembryonic whorls are hair brown axially streaked with benzo brown, and spirally lined with pale pinkish cinnamon or white faintly shaded with pallid mouse gray; on the last half whorl the light lines or bands are pallid mouse gray.

A sinistral shell (pl. 9, fig. 25*b*) resembles *A. a. versicolor* (pl. 9, fig. 22). The postembryonic whorls below the white subsutural band are benzo brown axially streaked with light drab, last whorl just above and all below the periphery wood brown axially streaked and spirally lined with tilleul buff. The shell may have a lined pattern (pl. 9, fig. 24); embryonic whorls naples yellow, lined with white on the last half whorl; postembryonic whorls lined with natal brown; lip and columella callus white, with the outer edge light vinaceous fawn. The lightest color pattern and an obese dextral (pl. 9, fig. 24*a*) measures: Length 18.0 mm., greater diameter 13.2 mm., spire height 9.6 mm. Postembryonic whorls white, banded at the suture and just above the edge of the periphery with light drab, base drab gray, lined with white.

**ACHATINELLA APEXFULVA WAHIAWA, new subspecies**

PLATE 2, FIGURE 36; PLATE 11, FIGURES 1-1*b*

*Achatinella swiftii* NEWCOMB, Pilsbry and Cooke, Man. Conch., vol. 22, pp. 312, 313, pl. 58, fig. 8; pl. 59, fig. 2*a* (only), 1914.

Gulick called this race of shells *A. pica*. Pilsbry and Cooke correctly consider the name *pica* a synonym of *A. a. apexfulva*. The form is a distinct lowland one which probably occurred at some low elevation below areas 90 and 91?? (fig. 5*a*, p. 105). *A. a. wahiarva* resembles *A. a. coniformis* but differs in usually being more strongly axially streaked, lacking pronounced fine spiral lines, and having white embryonic whorls. The shell is usually dextral.

The holotype (pl. 2, fig. 36) has white embryonic whorls darkening to pale pinkish buff on the last embryonic whorl; the first two and three-fourths postembryonic whorls vinaceous buff axially streaked with rood's brown, last whorl avellaneous axially streaked and spirally banded and lined with benzo brown and cameo brown; impressed sutural band mikado brown darkening on the last half whorl to walnut

brown; lip and columella callus white with a faint tint of seashell pink. Length 17.8 mm., greater diameter 12.5 mm., spire height 9.6 mm., number of whorls  $6\frac{1}{4}$ .

Distribution, area?: **Wahiawa, Gulick.**

The spire may be more concave (pl. 11, fig. 1a), the embryonic whorls more pointed, and the last whorl flattened and less rounded at the edge of the periphery than the holotype; the color pattern is similar to that of the holotype. A narrow specimen (pl. 11, fig. 1) and light color pattern measures: Length 17.1 mm., greater diameter 12.0 mm., spire height 9.4 mm.; first half postembryonic whorl pale pinkish buff axially streaked with warm buff, next whorl and a half pale vinaceous fawn axially streaked with light drab, last whorl seashell pink, axially streaked with vinaceous fawn and fawn color, at the edge of the periphery and about the base a line of benzo brown, in the umbilical region a patch of chamois.

A dark color pattern (pl. 6, fig. 1b) is figured, showing the dorsal side of the shell, to exhibit the contrast between the white embryonic whorls and the postembryonic whorls; the last half of the first postembryonic whorl and the penultimate whorl light cinnamon drab, finely axially streaked with dark vinaceous brown, first half of last whorl drab axially streaked with dark vinaceous brown, last half whorl almost solid dark vinaceous brown streaked with drab; impressed sutural band walnut brown. Length 16.5 mm., greater diameter 12.6 mm., spire height 9.1 mm.

#### GROUP OF A. A. LILACEA GULICK

#### ACHATINELLA APEXFULVA GULICKII Smith

##### PLATE 10, FIGURES 14-15b

*Apex gulickii* SMITH, Proc. Zool. Soc. London, 1873, p. 78, pl. 9, fig. 19 (not fig. 17).

*Achatinella apexfulva apicata* (Newcomb) PFEIFFER, Pilsbry and Cooke, Man. Conch., vol. 22, pp. 325, 326, 327, pl. 58, fig. 10a (?); pl. 60, figs. 6, 6a, 12 (only), 1914.

*A. a. gulickii* is characterized by having a white or light peripheral band and a grayish or gray-brown color pattern. The holotype (pl. 10, fig. 14) has the embryonic whorls cartridge buff; first half postembryonic whorl cinnamon buff darkening to cameo brown on the last half of the whorl, penultimate whorl drab gray axially streaked with benzo brown, last whorl pinkish buff above the peripheral band of gull gray axially streaked with benzo brown and light drab, below the periphery a band of benzo brown, below which is a band of pale

gull gray spirally lined with benzo brown, about the umbilicus a faint band of cartridge buff; impressed sutural band on the first half postembryonic whorl same as the ground color, on the remaining whorls pecan brown lightening to cinnamon on the last whorl; lip and columella callus light vinaceous cinnamon. Length 18.2 mm., greater diameter 12.3 mm., spire height 8.8 mm., number of whorls 6.

Distribution, area?: Type locality **Kalaikoa**, Gulick. Also reported from **Ahonui**, Gulick. The type locality was probably a restricted locality somewhere between North and South Kaukonahua Streams.

The color pattern of the holotype is an unusually dark gray pattern. A more usual one in the Gulick lots (pl. 10, fig. 15) has cream-buff embryonic whorls darkening to chamois on the last half embryonic whorl; postembryonic whorls pale vinaceous fawn axially streaked with vinaceous drab and pale brownish drab, peripheral band and base white, subperipheral band light brownish drab; impressed sutural band pinkish cinnamon lightening on the following whorls to pale ochraceous buff.

The darkest color pattern (pl. 10, fig. 15a) has the first two embryonic whorls cartridge buff darkening to chamois on the last embryonic whorl; postembryonic whorls pale quaker drab axially streaked with anthracene purple, on the last whorl about the periphery a line of white, last fourth whorl pinkish buff axially streaked with cinnamon drab, lip not formed. Another shell has a yellowish pink hue (pl. 10, fig. 15b); postembryonic whorls up to the last whorl vinaceous drab axially streaked with light pinkish cinnamon, last whorl light pinkish cinnamon streaked with vinaceous drab, peripheral band white; impressed sutural band vinaceous cinnamon.

#### ACHATINELLA APEXFULVA GULICKII var. 1

PLATE 10, FIGURE 16, 16a

*Achatinella apexfulva apicata* (Newcomb) PFEIFFER, Pilsbry and Cooke, Man. Conch., vol. 22, pp. 325, 326, pl. 60, figs. 11, 13 (only), 1914.

Area?: **Ahonui**, Gulick.

This light pinkish variety looks like an intermediate race between *A. a. gulickii* and *A. a. lilacea*, and is considered a variety of *A. a. gulickii* because of the light band just below or at the edge of the periphery of the last whorl.

The usual form and color pattern (pl. 10, fig. 16) has the embryonic whorls cartridge buff; first postembryonic whorl and a half vinaceous fawn axially streaked with pale brownish drab, last whorl and a half pale ecru drab axially streaked with white and faintly banded above



the periphery with pale vinaceous fawn, on the last whorl a peripheral band of white, base white, subperipheral band pale ecru drab; impressed sutural band pale vinaceous fawn; lip and columella callus white faintly tinted with pale vinaceous fawn. Length 19.0 mm., greater diameter 12.8 mm., spire height 10.4 mm., number of whorls  $6\frac{1}{2}$ .

The color may be light pink (pl. 10, fig. 16a) and the color pattern may resemble that of *A. a. lilacea* (pl. 10, fig. 10), although differing in having the last whorl, just below the periphery and at the base, banded and lined with white.

**ACHATINELLA APEXFULVA GULICKII var. 2**

PLATE 10, FIGURES 21-21b

*Achatinella swiftii* NEWCOMB, Pilsbry and Cooke, Man. Conch., vol. 22, pp. 309, 312, 315, pl. 58, figs. 13-13b; pl. 59, fig. 4e (only), 1914.

Area?: Kalaikoa, Gulick.

The form was described by Smith as a variety of *A. a. gulickii*. It is probably an intermediate race between *A. a. gulickii* var. 1 and *A. a. flavida*. The postembryonic whorls are of a pinkish color above the periphery, last whorl at and below the periphery banded with yellow.

The usual color pattern (pl. 10, fig. 21) on 37 percent of the shells has the embryonic whorls white, shading to cream buff on the last half embryonic whorl; first half postembryonic whorl vinaceous fawn with a central line of pale pinkish cinnamon, the remaining postembryonic whorls vinaceous pink, lined and axially streaked with pale pinkish cinnamon, the last whorl is tinted with chamois, a band of fawn color below the pale pinkish cinnamon band just below the edge of the periphery, base cream buff tinged with chamois; impressed sutural band pale pinkish cinnamon; lip and columella callus a very dilute tint of a pink or tilleul buff.

Thirty-three percent have a lighter or yellow color pattern (pl. 10, fig. 21a); the first postembryonic whorl and a half pale drab gray axially streaked with light cinnamon drab, first half of last whorl above the periphery pale drab gray tinged with chamois, last half almost entirely chamois, base chamois below the peripheral band of chamois, subperipheral band a faint shade of drab gray covered over by the ground color; impressed sutural band pale pinkish cinnamon.

A sinistral specimen (pl. 10, fig. 21b) shows the dark form of 30 percent of the shells; postembryonic whorls above the periphery fawn color; impressed sutural band fawn color; subsutural band or

line on the last two whorls white, shading to chamois on the last half whorl; the last half whorl is tinted with chamois, last whorl below the narrow peripheral band of white is chamois with a central band of fawn color.

ACHATINELLA APEXFULVA FLAVIDA Gulick

PLATE 10, FIGURES 17-20

*Apex flavidus* GULICK, Proc. Zool. Soc. London, 1873, p. 80, pl. 10, figs. 1, 1a.  
*Achatinella swiftii* NEWCOMB, Pilsbry and Cooke, Man. Conch., vol. 22, pp. 306, 311, 312, 315, pl. 58, figs. 10, 12-12b (only), 1914.

The subspecies is characterized by having a light yellow color pattern. The form of the shell resembles *A. a. gulickii* var. 2. The holotype is a rare color pattern and not characteristic of the subspecies. The holotype of *A. a. flavida* (pl. 10, fig. 17) has the first embryonic whorls a very dilute shade of pale ecru drab, fading to white; postembryonic whorls white, first postembryonic whorl with a cinnamon-buff suprapерipheral line which widens on the last two whorls to a band of mikado brown or walnut brown; the impressed sutural band white on the first embryonic whorl, on the last two whorls mikado brown darkening to cacao brown, base cartridge buff; columella callus pale pinkish cinnamon; lip cartridge buff. Length 19.8 mm., greater diameter 12.8 mm., spire height 10.7 mm., number of whorls  $6\frac{1}{2}$ .

Distribution, area?: Type locality **Kalaikoa**, Gulick (probably somewhere in South Kaukonahua Stream at a low elevation). Also Ahonui, Gulick, which is probably erroneous if Kalaikoa is correct, because the type locality was probably of limited extent.

Gulick's var. a (pl. 10, fig. 18) has a more usual color pattern; first embryonic whorl and a half white, shading to cream buff on the later embryonic whorls; first two postembryonic whorls pinkish buff axially streaked with cinnamon buff and mikado brown; below the impressed sutural band of tawny, which darkens on the last two whorls and a half to orange cinnamon, there is a band of white; on the penultimate whorl there is another band of white just above the edge of the periphery, last whorl chamois spirally banded with sayal brown. Length 17.6 mm., greater diameter 12.2 mm., spire height 9.3 mm., number of whorls 6. This color pattern occurs on 34 percent of the combined Kalaikoa and Ahonui lots, all but 7 of which are from Kalaikoa.

The usual color pattern in the Bishop Museum lots of the Gulick collection (pl. 10, fig. 19) has the embryonic whorls white, post-

embryonic whorls white up to the last whorl, last whorl above the periphery cream buff, with a band made up of fine drab-gray lines which darken on the last half whorl to cinnamon drab, above the band a line of avellaneous, below and at the edge of the periphery chamois, banded about the center of the base with two bands or lines of natal brown; impressed sutural band russet; lip and columella callus a very dilute shade of vinaceous fawn.

The shell may not be strongly ornamented with gray or brown lines or bands (pl. 10, fig. 19a), the first postembryonic whorl white spirally lined with warm sepia, penultimate whorl white, last whorl mustard yellow faintly banded with bands slightly darker than the ground; impressed sutural band on the first two postembryonic whorls russet, on the first half of the last whorl white with upper edge russet, on the last half whorl white. This color pattern occurs on 23 percent of the shells.

A variation of the usual color pattern (pl. 10, fig. 19b) has the first postembryonic whorl and half army brown with a subsutural line of white, and another line of white just above the periphery which broadens on the last half of the penultimate to a band, so that the whorl is white with a median band of army brown on the last half of the penultimate, last whorl, above the white peripheral band or line, banded with a white subsutural band, a band of army brown, and a band of chamois, on the last half whorl subsutural band tinted with chamois, below the periphery the ground chamois, with a central line of army brown.

In other lots of shells from Ahonui and Kalaikoa sometimes marked by Gulick "*tuberans-tumefacta*," is a white shell (pl. 10, fig. 20) which is banded on the postembryonic and on the impressed sutural band with pecan brown. I believe that this rare color pattern is a light color pattern of *flavida* which lacks the usual yellow color. Pilsbry and Cooke (pl. 58, fig. 10) figured a sinistral shell with this color pattern.

#### ACHATINELLA APEXFULVA LILACEA Gulick

PLATE 3, FIGURE 2; PLATE 10, FIGURES 8-11

*Apex lilaceus* GULICK, Proc. Zool. Soc. London, 1873, p. 79, pl. 10, fig. 4.

*Achatinella apexfulva apicata* (Newcomb) PFEIFFER, Pilsbry and Cooke, Man.

Conch., vol. 22, pp. 325, 328, pl. 60, figs. 14, 14a (only), 1914.

The holotype of *A. a. lilacea* (pl. 10, fig. 8) has the embryonic whorls white; postembryonic whorls white axially streaked with light vinaceous fawn darkening to vinaceous fawn on the last whorl;

impressed sutural band white; lip and columella callus light vinaceous fawn. Length 20.2 mm., greater diameter 13.2 mm., spire height 10.7 mm., number of whorls  $6\frac{1}{2}$ .

Distribution, area 83b??: Type locality **Kalaikoa**, Gulick; also **Ahonui**, Gulick. The type locality containing a pure race of pink shells of the typical *A. a. lilacea* pattern has not been located in recent years. Meinecke in locality 280\* (fig. 5, p. 105), **North Kaukonahua-Poamoho Ridge**, BBM 121982, found two specimens of typical *A. a. lilacea* mixed with *A. a. lilacea* var. 1. This indicates that Gulick's type locality was probably somewhere in the region of North Kaukonahua Stream which was all or part of Gulick's Ahonui, and not in Kalaikoa. The possible region of the type locality area 83b?? has been plotted on figure 7, (p. 194).

The usual form of *A. a. lilacea* (pl. 3, fig. 2) has the embryonic whorls pale pinkish buff; postembryonic whorls seashell pink axially streaked with buff pink; impressed sutural band white; lip and columella callus shell pink. Length 18.7 mm., greater diameter 12.2 mm., spire height 10.0 mm., number of whorls 6. A narrow specimen (pl. 10, fig. 9) measures: Length 18.0 mm., greater diameter 11.8 mm., spire height 11.0 mm. An obese specimen (pl. 10, fig. 10) measures: Length 18.2 mm., greater diameter 12.8 mm., spire height 10.0 mm. The color pattern of figures 9 and 10 is similar to that of plate 3, figure 2, except that the impressed sutural band is the same as the rest of the whorl.

One of the Meinecke pink shells (pl. 10, fig. 11) from locality 280\* has the embryonic whorls white; postembryonic whorls pale salmon color; impressed sutural band the same as the rest of the whorl.

#### ACHATINELLA APEXFULVA LILACEA var. 1

PLATE 3, FIGURE 3; PLATE 10, FIGURES 12-13

Area 83: **North Kaukonahua-Poamoho Ridge**, locality 280-1-280\*, approximate elevation 1,450 feet, Russ, 1929-1933; 280\*, elevation 1,350-1,450 feet, Meinecke, 1932. Also collected by Wilder, BBM 50585.

Area 83a: **North Kaukonahua-Poamoho Ridge**, locality 281-2\*, elevation 1,500 feet, 1932, BBM 121987, 121988; 281-1, elevation 1,500-1,550 feet, Meinecke, 5 dextral 1933 (figs. 5, 5a, p. 105). Locality 281-2\*, plotted from memory, probably should be below locality 281-1.

The shell is very similar in form and color pattern to typical *A. a. lilacea*, differing in having a bluish-gray hue instead of a pinkish color pattern. This race is probably intermediate between *A. a. lilacea* and *A. a. lilacea* var. 2.

The usual color pattern and form of the shell (pl. 10, fig. 12) has the embryonic whorls white; postembryonic whorls pale vinaceous fawn axially streaked with light vinaceous fawn on the first postembryonic whorl and light cinnamon drab on the penultimate, last whorl ecru drab axially streaked with cinnamon drab and benzo brown and faintly spirally lined and axially streaked with tilleul buff; impressed sutural band same as the rest of the whorl, upper edge white; lip and columella callus pale grayish vinaceous. Length 19.0 mm., greater diameter 12.0 mm., spire height 10.9 mm.

An obese shell (pl. 10, fig. 12a) measures: Length 17.8 mm., greater diameter 12.7 mm., spire height 9.1 mm.; shows a very light color form; first half postembryonic whorl pale pinkish buff, next whorl and a quarter up to the last whorl light vinaceous fawn axially streaked with a dilute shade of vinaceous fawn, last whorl pale ecru drab axially streaked with cinnamon drab and tilleul buff on the last whorl; impressed sutural band white. White sutural bands occur on one or two specimens in each lot.

In the Russ lot from locality 280-1-280\*, 66 percent are pinkish forms (pl. 10, fig. 12) and 36 percent bluish-gray forms (pl. 10, fig. 12b; pl. 3, fig. 3). In the Meinecke lot from 280\*, 56 percent are pinkish forms and 44 percent bluish pink. Locality 281-2\*, has 71 percent bluish forms, and 281-1 contains no pink forms. These last two localities have been separated out into area 83a to emphasize the trend toward bluish-gray color forms above area 83. More collecting should be done in this region to determine whether bluish-gray shells exist in a pure locality below area 84 where the streaked color pattern changes but the color is definitely bluish gray.

The usual color pattern and form of a bluish-gray shell (pl. 3, fig. 3) has the embryonic whorls pale pinkish buff; first postembryonic whorl pale pinkish buff, last two whorls pale mouse gray axially streaked with quaker drab, sorghum brown, and tilleul buff, last fourth whorl tilleul buff axially streaked with avellaneous; impressed sutural band tilleul buff axially streaked with vinaceous buff; lip and columella callus light vinaceous fawn. Length 19.0 mm., greater diameter 12.0 mm., spire height 10.5 mm. The color of the sutural band is unusual.

The color pattern may be lighter, the form elongate and the impressed sutural band white (pl. 10, fig. 12b), which is usual; embryonic whorls white; first half postembryonic whorl white, last half white axially streaked with light vinaceous fawn, penultimate and last whorl pale drab gray axially streaked with pale brownish drab and light brownish drab; lip and columella callus light vinaceous fawn.



Length 19.0 mm., greater diameter 12.0 mm., spire height 10.8 mm. Plate 10, figure 13, shows a sinistral shell from area 83a which has the same color pattern as plate 10, figure 12b.

**ACHATINELLA APEXFULVA LILACEA** var. 2

PLATE 3, FIGURE 4

Area 84: **North Kaukonahua-Poamoho Ridge**, locality 282-1, elevation 1,600 feet, 3 dextral; 282-3, elevation 1,550 feet, 10 dextral, all collected by Meinecke, 1933 (figs. 5, 5a, p. 105).

Out of 13 shells from area 84, 3 have pink color patterns similar to the shells of area 83. The remainder have a bluish-gray color pattern which differs from the forms of area 83a by having a yellowish ground color and the last whorl more strongly spirally lined.

The usual color pattern (pl. 3, fig. 4) has the embryonic whorls light buff; first half postembryonic light buff axially streaked with cinnamon buff, next whorl light cinnamon drab, last whorl and a half light buff axially streaked and faintly spirally lined with hair brown, also streaked with benzo brown; impressed sutural band light buff; lip and columella callus white, lip edged with avellaneous.

**ACHATINELLA APEXFULVA GLAUCOPICTA**, new subspecies

PLATE 3, FIGURE 10; PLATE 10, FIGURES 22, 22a

*Achatinella apexfulva cervixnivea* pattern Pilsbry and Cooke, Man. Conch., vol. 22, pp. 324, 328, pl. 60, fig. 9 (only), 1914.

The shell resembles the blue-gray color pattern of *A. a. lilacea* var. 1 but differs in having a sutural band which is always white, more bluish postembryonic whorls, stronger blue-gray axial streaks, and the ground pale gray instead of pinkish.

The embryonic whorls of the holotype (pl. 3, fig. 10) are white, postembryonic whorls white axially streaked with pale neutral gray and deep neutral gray; impressed sutural band white; lip and columella callus pale grayish vinaceous. Length 19.4 mm., greater diameter 13.1 mm., spire height 10.4 mm., number of whorls  $6\frac{1}{4}$ . The usual form was not determined for lack of specimens.

Distribution, area 87: **Central Poamoho Stream**, type locality 280K-2, elevation 1,250 feet, Meinecke, 1933; **Central Poamoho-Central Poamoho North Branch Ridge**, 280L-1, elevation 1,450-1,500 feet, 5 dextral and 1 sinistral, Meinecke, 1933 (figs. 5, 5a, p. 105).

The darkest color pattern (pl. 10, fig. 22) has the postembryonic whorls plumbeous axially streaked with white, dark violet gray, and blackish violet gray, last whorl almost solid blackish violet gray axially streaked by the above lighter shades of gray; impressed sutural band white; lip and columella callus light vinaceous fawn.

The usual form of a sinistral, shown on plate 10, figure 22a, has a color pattern similar to plate 3, figure 10, except that the dark axial streaks are finer and resemble those of *A. a. lilacea* var. 1 (pl. 3, fig. 3).

**ACHATINELLA APEXFULVA PUNICEA, new subspecies**

PLATE 2, FIGURE 26; PLATE 10, FIGURES 6-6c

The shape is similar to the probably lower race of *A. a. steeli*, but the color pattern is different. The color pattern resembles that of *A. a. lilacea*, but the range of color pattern and the form of the shell make it distinct from *lilacea*, which is a much smaller shell. The embryonic whorls of the holotype (pl. 2, fig. 26) are white, shading to pale pinkish buff on the last embryonic whorl; postembryonic whorls vinaceous buff axially streaked with avellaneous and tilleul buff; impressed sutural band light buff, tinting to pale pinkish buff on the last half whorl; lip and columella callus light vinaceous fawn lightening to white within. Length 19.0 mm., greater diameter 13.3 mm., spire height 9.6 mm., number of whorls 6.

Distribution, area 81??: **Kaukonahua**, Wilder, BBM 50583, 50581; also collected by O. P. Emerson on "Head gate road ridge between N. & S. br. of Kaukonahua," in the collection of the MCZ. The type locality is not known exactly. Odd specimens with the usual *A. a. punicea* pattern are found with *A. a. steeli* in locality 272. In the type lot a few blue-gray shells are found which are similar to *A. a. punicea* var. 1 (area 82?). The subspecies *A. a. punicea* probably exists somewhere between areas 80 and 82?, probably near the bottom of North Kaukonahua Stream, in the region of area 81?? (fig. 5a, p. 105).

An obese shell (pl. 10, fig. 6) measures: Length 19.4 mm., greater diameter 13.5 mm., spire height 8.9 mm.; embryonic whorls light buff; postembryonic whorls wood brown faintly axially streaked with tilleul buff, about the periphery a band of tilleul buff; impressed sutural band a hue between cinnamon and avellaneous; lip and columella callus pale vinaceous fawn. The pink color pattern of the holotype and plate 10, figure 6 occurs on 59 percent of the shells.

The sutural band may be white, the form elongate, and the color pattern a bluish pink (pl. 10, fig. 6a) intermediate between *A. a.*

*punicea* and *A. a. punicea* var. 1. The embryonic whorls are white; postembryonic whorls pale ecru drab axially streaked and faintly finely lined with pale brownish drab; lip and columella callus pale vinaceous fawn, the outer margin vinaceous fawn. Length 20.5 mm., greater diameter 13.0 mm., spire height 10.8 mm. This pattern is present on 39 percent of the shells. One specimen in the type lot is almost entirely white (pl. 10, fig. 6*b*), last whorl shaded with axial streaks of pale salmon color. In lot BBM 50581, out of seven shells, three are pinkish forms and three are bluish pink, and one has a yellowish pattern (pl. 10, fig. 6*c*); embryonic whorls light buff; postembryonic whorls light buff axially streaked with a dilute tint of pinkish cinnamon.

**ACHATINELLA APEXFULVA PUNICEA var. 1**

PLATE 2, FIGURE 27; PLATE 10, FIGURES 7-7*b*

Area 82?: North-South Kaukonahua Ridge, Lemke, BBM 115039, 1932, exact locality not accurately plotted but probably somewhere in the region of area 82?, but may have been collected at a higher or a lower elevation; also collected by Wilder, BBM 50578, but the shells have no locality label. Probably collected in or near area 82?, or in North Kaukonahua Stream (fig. 5*a*, p. 105).

The shell resembles *A. a. punicea* in form and size but differs in having a blue-gray color pattern similar to that of *A. a. glaucopicta*. A shell with the characteristic color pattern (pl. 2, fig. 27) has the first embryonic whorl and a half worn, colored cinnamon buff, remaining embryonic whorls pale pinkish buff; first postembryonic whorl white faintly axially streaked on the last half whorl with pale drab gray, penultimate whorl pallid mouse gray, finely axially streaked with white, and coarsely axially streaked on the last half with quaker drab, last whorl pallid mouse gray axially streaked with deep quaker drab, last fourth whorl hair brown axially streaked with fuscous; impressed sutural band white. Length 20.5 mm., greater diameter 13.3 mm., spire height 11.1 mm. The usual form of the shell was not obtainable owing to scarcity of material.

In the Wilder lot, BBM 50578, the lightest color pattern (pl. 10, fig. 7) has a pinkish tint and occurs on 17 percent of the shells. The postembryonic whorls shade from white to pale vinaceous fawn on the last two whorls, faintly lined and axially streaked with pale drab gray; impressed sutural band white. Length 18.5 mm., greater diameter 13.1 mm., spire height 9.0 mm. A sinistral shell (pl. 10, fig. 7*a*) has the embryonic whorls light buff; first postembryonic

whorl, below the white sutural and subsutural bands, light mouse gray, last whorl and a half pale vinaceous fawn axially streaked and faintly spirally lined with pale brownish drab; lip and columella callus pale vinaceous fawn. Forty-seven percent of the Wilder lot have yellow embryonic whorls. The darkest color pattern (pl. 10, fig. 7*b*), found on two shells, has the embryonic whorls white; post-embryonic whorls dark vinaceous drab axially streaked with drab gray, last half whorl mostly drab gray axially streaked with dark vinaceous drab; impressed sutural and subsutural bands white. The subsutural band, as in all specimens of this variety, decreases in width on each successive whorl so that it is lacking or merely a line on the last whorl.

**ACHATINELLA APEXFULVA STEELI, new subspecies**

PLATE 2, FIGURE 25; PLATE 10, FIGURES 3-5*c*

*Achatinella apexfulva apicata* NEWCOMB, Pilsbry and Cooke, Man. Conch., vol. 22, p. 325, pl. 60, figs. 5*b*, 10, 1914.

The color pattern of the shell resembles *A. a. gulickii* but differs in being a larger shell with a dark reddish-brown color pattern. The embryonic whorls of the holotype (pl. 2, fig. 25) are pale pinkish buff; last half of the first postembryonic and penultimate whorls chocolate axially streaked and spirally banded with cinnamon drab, last whorl above the periphery light drab spirally lined and banded with chocolate, subperipheral band lilac buff, axially streaked with light drab and on the last half whorl streaked with avellaneous, base light drab axially streaked with white, spirally banded with natal brown and bone brown; lip and columella callus fawn color lightening to light vinaceous fawn on the inner margin. Length 19.3 mm., greater diameter 13.0 mm., spire height 10.2 mm., number of whorls 6½.

Distribution, area 80: **North-South Kaukonahua Ridge**, type locality 271, elevation 1,450-1,532 feet, Russ, 1933. Steel BBM 129017-129018, 6 sinistral 1934; also 272, elevation 1,500-1,550 feet, 1 dextral, 7 sinistral, Steel and Welch, 1934. Also collected by Gulick, O. H. Emerson, BBM 103972. Wilder, BBM 50577, 50580 (figs. 5, 5*a*, p. 105). This subspecies is named after Lt. Col. Charles L. Steel, U. S. A., who helped me determine the distribution of certain forms of *Achatinella* and generously gave me valuable material.

The obese form of the shell (pl. 10, fig. 3) measures: Length 19.3 mm., greater diameter 13.5 mm., spire height 10.0 mm.; embryonic whorls pale pinkish cinnamon, lightening to white on the last embryonic whorl; first half postembryonic whorl cinnamon buff axially

streaked with mikado brown, remaining whorls chocolate, faintly axially streaked with pinkish buff, spirally lined on the upper third of the whorl above the periphery with a line of light drab and cinnamon, on the last half whorl above the periphery the chocolate ground color changing to buffy brown or olive brown axially streaked and banded with a band of bone brown, below the periphery a band of cartridge buff and a band of chocolate, the remainder of the base cartridge buff spirally lined with drab gray and two bands of natal brown in the umbilical region.

In the lot collected by Steel from locality 271 a gray color pattern is found (pl. 10, fig. 4); postembryonic whorls light drab axially streaked with hair brown, fuscous, benzo brown, and faintly spirally lined with fine lines of fuscous and white, below the periphery of the last whorl the ground white, shaded with pale gull gray and spirally banded with a band and a line of light drab axially streaked with fuscous, in the umbilical region a line and a band of fawn color.

In the Wilder collection, mixed with color patterns of typical *A. a. steeli*, are a series of color patterns which have the base white or banded with white below the periphery and contain dextral as well as sinistral shells. The shells may be typical *A. a. steeli* or they may come from a different area.

The usual form of a dextral shell and a characteristic color pattern in this lot (pl. 10, fig. 5) has the embryonic whorls cartridge buff; postembryonic whorls pecan brown, spirally ornamented on the last whorl and a half with a white band or line, below the impressed pecan brown sutural band and in the center of the whorl above the periphery, edge of the periphery banded with a wide white band, at the upper edge of which is a line of pecan brown, remainder of the base white with a central band and a line of pecan brown, in the umbilical region a patch of fawn color; lip and columella callus pale vinaceous fawn, outer margin spotted with fawn. Length 20.0 mm., greater diameter 13.0 mm., spire height 10.6 mm.

The base may be entirely white (pl. 10, fig. 5a) faintly shaded with vinaceous fawn and lined with a line of army brown in the umbilical region; the postembryonic whorls above the periphery are similar to plate 10, figure 5, only more axially streaked and spirally lined with white. A narrow sinistral specimen (pl. 10, fig. 5b) measures: Length 18.4 mm., greater diameter 12.2 mm., spire height 9.7 mm. An obese shell (pl. 10, fig. 5c) measures: Length 18.0 mm., greater diameter 13.6 mm., spire height 9.0 mm. The shells of figures 5b and 5c have a similar color pattern to the shell of plate 10, figure 3.



**ACHATINELLA APEXFULVA STEELI var. 1**

PLATE 2, FIGURE 24; PLATE 10, FIGURES 1-2

Area 79: North-South Kaukonahua Ridge, locality 270, elevation 1,450 feet, 3 dextral, dead specimens, Steel and Welch, BBM 129012, 1934; "Mauka [toward the mountains] of the Burnt District, Kaukonahua," Thurston, BBM 130674. The burnt district is in the region of area 78?, on the North-South Kaukonahua Ridge. Also collected by Wilder, BBM 10446, Lemke, BBM 115036, Gulick, BBM 10445 (figs. 5, 5a, p. 105).

This variety may be a distinct subspecies separable from *A. a. steeli* by having a distinctly lighter color pattern. The Welch lot of three shells indicates this possibility, but in all other lots the variety is found mixed with *A. a. steeli*. Therefore, until more careful collecting is done in area 79 and this race is definitely proved to be a distinct race and not a light color pattern of the shells of area 80, this form is considered a variety of *A. a. steeli*.

The usual form and color pattern of the shell (pl. 2, fig. 24) has the embryonic whorls pale pinkish buff; the upper half of the first two postembryonic whorls including the impressed sutural band cameo brown, lower half white, banded just above the edge of the periphery with a band of vinaceous buff lined with army brown, this band fading to white on the last half of the penultimate, the last whorl white, sutural and subsutural bands chocolate, subsutural band lined with pale pinkish cinnamon, below the subsutural band a band of tawny lined with russet, above the peripheral line of tawny the white supraperipheral band shaded with cinnamon buff, below the periphery the ground white banded with army brown, base finely lined with pale brownish drab; lip outer margin vinaceous fawn, inner margin and columella callus white. Length 18.8 mm., greater diameter 12.8 mm., spire height 9.8 mm., number of whorls  $6\frac{1}{2}$ .

A narrow form with a narrow sutural band (pl. 10, fig. 1) has the embryonic whorls white; postembryonic whorls white, banded below the burnt umber sutural band with a band of white, burnt umber, and sayal brown, on the last whorl the sayal brown band lightening to cinnamon buff and fading out on the last half whorl, the white ground shaded by faint bands of pinkish buff, base lined with fawn color. Length 18.3 mm., greater diameter 12.0 mm., spire height 10.4 mm.

A sinistral specimen (pl. 10, fig. 1a) resembles the pattern of plate 2, figure 24, on the first two postembryonic whorls; last whorl pale pinkish cinnamon, below the subsutural bands of chocolate and pinkish cinnamon, spirally banded at and above the periphery with

light buff which deepens to warm buff on the last whorl, below the periphery base banded with a band of cinnamon drab, benzo brown and cream color in the umbilical region.

A possible intermediate pattern between *A. a. versicolor* var. 1 and *A. a. steeli* var. 1 (pl. 10, fig. 1b) is seen on three specimens in the Wilder collection; embryonic whorls white; postembryonic whorls banded at the suture and below the suture by a wide band of chestnut brown covering the upper half of the whorl, which is solid or lined with drab gray, just above the edge of the periphery a band of pale ecru drab axially streaked with white and spirally lined with light brownish drab, just below the edge of the periphery a band of white and below this a band of natal brown, base white, shaded with ecru drab and lined with a line of light brownish drab.

In the Thurston lot there is a very light color pattern (pl. 10, fig. 2). The embryonic whorls are pale pinkish cinnamon; first postembryonic whorl pale pinkish cinnamon, banded with bone brown, and cinnamon, penultimate and last whorl white, banded above or at the edge of the periphery with a narrow band of bone brown lightening to army brown, above the peripheral band a faint band of cinnamon buff, below the periphery the ground white lined and banded with avellaneous; lip and columella callus avellaneous lightening to white toward the inner margin. Before the Thurston collection was given to the Bishop Museum the cabinets containing the collection were moved during a fire. In moving the cabinets they were tilted and shells from different localities were mixed. Therefore the exact location of this light color form should be checked.

#### GROUP OF *A. a. APICATA* NEWCOMB

#### **ACHATINELLA APEXFULVA BRUNOSA**, new subspecies

PLATE 3, FIGURE 11; PLATE 10, FIGURES 26-28

This species is similar to *A. a. lilacea* var. 1 (area 83) in form, in the width of the axial streaks on the postembryonic whorls, and in usually having a white sutural band. It differs in having the last whorl and a half gray or gray brown. *A. a. brunosa* also closely resembles *A. a. apicata*, but differs in the shade of brown of the postembryonic whorls, and in usually having a white sutural band.

The first two postembryonic whorls of the holotype (pl. 3, fig. 11) are cinnamon pink, deepening on the last embryonic whorl to ochraceous buff, first half postembryonic whorl army brown axially streaked with white, next whorl axially streaked with pale gull gray and deep neutral gray, next half whorl finely axially streaked with

hair brown, and smoke gray, last whorl drab finely axially streaked with hair brown; impressed sutural band upper two-thirds white, lower third the color of the whorl below; lip and columella callus light vinaceous fawn. Length 18.9 mm., greater diameter 12.3 mm., spire height 10.8 mm., number of whorls 6.

Distribution, area 88: **Central Poamoho-Central Poamoho North Branch Ridge**, type locality 280L-2, elevation 1,550 feet; also 280L-3, elevation 1,600-1,650 feet, 2 dextral, 5 sinistral, Meinecke, 1933; 280L-4, elevation 1,700 feet; 280L-5, elevation 1,650 feet, 18 sinistral, all Meinecke-collected, 1933 (figs. 5, 5a, p. 105).

An extremely narrow shell (pl. 10, fig. 26) shows a lighter color pattern; first half postembryonic whorl army brown axially streaked with white, next whorl axially streaked with hair brown, benzo brown, white, and pale pinkish cinnamon, first half of last whorl the ground above the periphery pale pinkish cinnamon darkening on the last half whorl and below the periphery to a yellowish hue of wood brown, the entire whorl axially streaked with snuff brown and warm sepia; impressed sutural band white. Length 18.5 mm., greater diameter 11.6 mm., spire height 10.5 mm.

On one specimen the sutural band is found to be mikado brown on the last two whorls. This obese shell (pl. 10, fig. 26a) resembles more the form and color pattern of *A. a. suturafusca* var. 2 (pl. 10, fig. 25b). The first two postembryonic whorls and the last whorl above the periphery pallid mouse gray or mouse gray axially streaked with dark purple drab, last whorl below the periphery snuff brown on the last half of the whorl, last whorl below the periphery sayal brown axially streaked with bister or benzo brown. Length 20.0 mm., greater diameter 13.4 mm., spire height 11.2 mm.

The usual form of a sinistral and a grayish pattern (pl. 10, fig. 27) has the penultimate and first half of last whorl drab gray axially streaked with pale drab gray or white, last half of last whorl light drab darkening to drab axially streaked with hair brown and snuff brown, just above the edge of the periphery a line of white. Length 18.2 mm., greater diameter 12.1 mm., spire height 9.9 mm.

The color pattern of a sinistral (pl. 10, fig. 28) shows the darkest brownish color pattern with the usual fine axial streaks, of the subspecies. The first half of the first postembryonic whorl cinnamon buff, faintly axially streaked with army brown, last half livid brown lightly axially streaked with pallid mouse gray, penultimate whorl light mouse gray deepening to mouse gray, and axially streaked with

deep mouse gray, last whorl drab axially streaked with hair brown and fuscous, last fourth whorl sepia.

**ACHATINELLA APEXFULVA SUTURAFUSCA, new subspecies**

PLATE 3, FIGURE 9; PLATE 10, FIGURES 24, 24a

*Achatinella apexfulva apicata* (Newcomb) PFEIFFER, Pilsbry and Cooke, Man. Conch., vol. 22, p. 326, pl. 60, fig. 7b (only), 1914.

The shell resembles the form of *A. a. glaucopicta* but has a brown sutural band and yellow embryonic whorls. The first two embryonic whorls of the holotype (pl. 3, fig. 9) warm buff deepening to ochraceous buff on the last embryonic whorl; first half of first post-embryonic whorl white, next whorl and a half lilac gray axially streaked with violet gray, last whorl pale mouse gray axially streaked with deep mouse gray and tilleul buff, and faintly spirally lined with deep mouse gray with a spiral band of tilleul buff just above the edge of the periphery, last fourth whorl tilleul buff axially streaked with army brown; impressed sutural band chestnut; lip and columella callus pale vinaceous fawn. Length 19.1 mm., greater diameter 13.5 mm., spire height 9.3 mm., number of whorls 6½.

Distribution, area 86: **Central Poamoho Stream**, type locality 280K-1\*, elevation 1,150-1,250 feet, Meinecke, 1932 (figs. 5, 5a, p. 105). Also collected by O. H. Emerson, BBM 102289, Wilder, BBM 50586. The Wilder shells are labeled North Kaukonahua, probably an error for Central Poamoho Stream.

The lightest color pattern (pl. 10, fig. 24), found on only three specimens, has the first two postembryonic whorls white, the penultimate axially streaked with pale drab gray, last whorl a dilute shade of pale drab gray or white axially streaked with drab gray and faintly spirally banded, below the chestnut sutural band, with a wide band of a dilute shade of pale quaker drab, and a band of tilleul buff at the edge of the periphery.

The usual form and color pattern of a sinistral shell (pl. 10, fig. 24a) also exhibits the dark color pattern of a dextral shell, embryonic whorls ochraceous tawny; first postembryonic whorl light neutral gray axially streaked with white, penultimate whorl light neutral gray axially streaked with neutral gray and deep neutral gray and finely spirally lined with lines of deep neutral gray, last whorl mouse gray axially streaked and faintly spirally lined with deep mouse gray; impressed sutural band chestnut. Length 18.1 mm., greater diameter 12.3 mm., spire height 9.6 mm.

## ACHATINELLA APEXFULVA SUTURAFUSCA var. 1

PLATE 3, FIGURE 1; PLATE 10, FIGURE 23

*Achatinella apexfulva apicata* (Newcomb) PFEIFFER, Pilsbry and Cooke, Man. Conch., vol. 22, p. 326, pl. 60, fig. 7a (only), 1914.

Area 85: **South Poamoho Stream**, locality 280-7, elevation 1,300-1,350 feet, Welch and C. W. Isle, 8 sinistral 1935 (figs. 5, 5a, p. 105).

The form is close to typical *A. a. suturafusca*, but differs in having a mars brown impressed sutural band, and the postembryonic whorls not colored with as bluish-gray streaks as *A. a. suturafusca*. Moreover, the dark color pattern (pl. 10, fig. 23) is not known to me from area 86.

The light color form (pl. 3, fig. 1) has the embryonic whorls tawny; first fourth postembryonic whorl tawny, the remaining whorls tilleul buff or pale drab gray axially streaked with deep mouse gray and mouse gray, the last two whorls faintly spirally lined with deep mouse gray; lip and columella callus light grayish vinaceous. Length 19.8 mm., greater diameter 13.1 mm., spire height 10.6 mm. So few specimens are known from this area that the usual form and color pattern is not determined.

The dark color pattern (pl. 10, fig. 23) has the embryonic whorls amber brown; postembryonic whorls clove brown or black axially streaked with drab gray, last eighth whorl verona brown; impressed sutural band bone brown or black. Length 18.1 mm., greater diameter 12.7 mm., spire height 9.0 mm.

## ACHATINELLA APEXFULVA SUTURAFUSCA var. 2

PLATE 3, FIGURE 13; PLATE 10, FIGURES 25-25d

*Achatinella apexfulva apicata* (Newcomb) PFEIFFER, Pilsbry and Cooke, Man. Conch., vol. 22, p. 326, pl. 60, figs. 4, 7(?) (only), 1914.

Area 89: **North Poamoho Stream**, locality 290\*, elevation 1,300 feet, Meinecke, 1914, 1917, 4 dextral, 8 sinistral 1926; **Wahiawa**, Gulick, ANSP 92628 (figs. 5, 5a, p. 105).

This race is very similar to *A. a. suturafusca* (area 86) but differs in usually having a more purplish-gray or darker color pattern. Brownish color forms similar to *A. a. apicata* also occur in area 89 but not in area 86. The form also resembles *A. a. suturalba* but differs in having a brown sutural band. This variety is an intermediate one between *A. a. apicata* and *A. a. suturalba*.



The usual form and color pattern (pl. 3, fig. 13) has the embryonic whorls ochraceous tawny; first fourth postembryonic whorl cinnamon drab axially streaked with tilleul buff, next whorl and a fourth gull gray axially streaked and finely lined with vinaceous slate, last half of penultimate and first fourth of last whorl gull gray heavily axially streaked and finely lined with dusky drab, the second fourth of last whorl dark livid brown, last half whorl cinnamon drab axially streaked with deep brownish drab and faintly spirally banded or tinged with a faint tint of dark heliotrope gray; impressed sutural band pale ochraceous buff on the first two whorls spotted with cinnamon buff, on the last whorl the color is cinnamon; lip and columella callus light vinaceous fawn. Length 20.0 mm., greater diameter 13.1 mm., spire height 11.2 mm., number of whorls  $6\frac{1}{2}$ .

The darkest color pattern (pl. 10, fig. 25) and the obese form of the shell has the first three-fourths postembryonic whorl axially streaked with gull gray and dusky brown, the next or last whorl and a half is almost solid dusky brown with faint axial streaks and spiral lines of light quaker drab which are almost obsolete; impressed sutural band burnt umber. Length 18.8 mm., greater diameter 13.8 mm., spire height 9.3 mm. An extreme narrow shell and light grayish-brown pattern (pl. 10, fig. 25a) has the first postembryonic whorl and a half pale smoke gray axially streaked and faintly spirally lined with light grayish olive, the last whorl pale smoke gray spirally lined and axially streaked with hair brown, last one-fourth whorl tilleul buff axially streaked with verona brown. Length 17.8 mm., greater diameter 11.2 mm., spire height 10.2 mm.

Meinecke first collected locality 290\* in 1914 and obtained 109 shells, 93 percent of which are dextral. In 1917 he again went to the same region and collected 83 shells, 86 percent of which are sinistral. Since all Meinecke's plotting before 1933 is done from memory it is probable that these two lots represent slightly different localities. The sinistral lot appears to have more bluish forms than the lot of dextral shells. The usual dextral color patterns resemble typical *A. a. apicata*. It is possible that the dextral locality may be one closer to the area of *A. a. apicata* than the sinistral lot and so transitional specimens between the two forms are found.

The usual form of a dextral (pl. 10, fig. 25b) has the embryonic whorls ochraceous tawny; first postembryonic whorl and a half axially streaked with natal brown and pallid mouse gray, last whorl and a half hay's brown, axially streaked with tilleul buff, and sorghum brown and faintly spirally lined with benzo brown; impressed sutural band cinnamon; lip and columella callus a very dilute tint of pale

vinaceous fawn. Length 19.6 mm., greater diameter 13.1 mm., spire height 10.8 mm.

A narrow dextral and light bluish pattern (pl. 10, fig. 25c) has the first half postembryonic whorl pale ochraceous salmon, axially streaked with pale vinaceous fawn, next whorl and a half light neutral gray spirally lined and streaked with pale gull gray, on the last half whorl ground color pallid neutral gray almost covered over with closely set axial streaks of light purplish gray and purplish gray; impressed sutural band cinnamon, darkening to mikado brown on the last whorl. Length 19.8 mm., greater diameter 12.7 mm., spire height 11.1 mm.

One specimen was found with a pinkish pattern (pl. 10, fig. 25d), the last whorl and a half seashell pink streaked and spirally lined and banded with light mouse gray. This color pattern is found in lots of shells collected by Gulick, Thurston, and others. Possibly there is an intermediate region between areas 89 and 93 where *A. a. suturafusca* var. 2 intergrades with *A. a. cervinivea*.

#### ACHATINELLA APEXFULVA SUTURALBA, new subspecies

PLATE 3, FIGURE 12; PLATE 10, FIGURES 29, 29a

*Achatinella apexfulva apicata* (Newcomb) PFEIFFER, Pilsbry and Cooke, Man. Conch., vol. 22, p. 325, pl. 60, fig. 4b (only), 1914.

The form resembles *A. a. suturafusca* but differs in usually having a white sutural band instead of a brown sutural band. Gulick collected this form, but his lot (ANSP) contains a mixture of *A. a. suturafusca* var. 2 and *A. a. suturalba*. His material is probably a mixture of shells from areas 89 and 90 together with some intermediate localities between these two areas.

The embryonic whorls of the holotype (pl. 3, fig. 12) ochraceous tawny; first two postembryonic whorls axially streaked with pallid mouse gray, white, deep quaker drab, and quaker drab, last whorl axially streaked with dark vinaceous drab, pale drab gray, and on the last fourth of the whorl deep brownish drab; lip and columella callus white or faintly tinged with a pinkish shade, possibly pale vinaceous fawn. Length 19.4 mm., greater diameter 13.2 mm., spire height 10.8 mm., number of whorls 6½.

Distribution, area 90: **North Poamoho Stream**, type locality 290AA-8, elevation 1,150-1,200 feet, Lemke and Welch, 1935; also locality 290AA-5, elevation 1,150 feet, 1 dead dextral, Welch, BBM 132753, 1935; 291A-2, elevation 1,150 feet, 1 dead dextral, Welch, BBM 165914, 1935; **Central Poamoho Stream**, locality 280AA-2,

elevation 1,100 feet, 3 dead dextral, Welch, BBM 132771, 1935; also collected by Wilder, BBM 50636, Gulick, ANSP 98628C (figs. 5, 5a, p. 105).

The lightest color pattern found on only two specimens is shown on plate 10, figure 29; last two postembryonic whorls axially streaked with white, neutral gray, and deep neutral gray; impressed sutural band and also the subsutural band, which disappears on the last half whorl, white axially streaked with seashell pink; lip and columella callus light vinaceous fawn.

A narrow shell (pl. 10, fig. 29a) and a dark color pattern lacks the usual white sutural band; postembryonic whorls chaetura black axially streaked with white, or tilleul buff; impressed sutural band tilleul buff streaked with avellaneous. Length 20.0 mm., greater diameter 12.2 mm., spire height 12.1 mm. This form with a colored sutural band occurs on five specimens in the combined Lemke and Welch lots of 45 shells exhibiting the color pattern. Fifty-one percent have a white sutural band, the rest a tinted sutural band similar to that of figures 29 or 29a.

**ACHATINELLA APEXFULVA SUTURALBA var. 1**

PLATE 3, FIGURE 19

Area 91??: **Helemano**, J. S. Emerson, BBM 102298-102299, also Gulick. Possibly this race occurred in the South Helemano opposite area 90 in area 91?? (fig. 5a, p. 105). No specimens have been found in recent years.

This variety is similar to *A. a. suturalba* but has a wider band of white about the suture and never has a dark or a pinkish sutural band similar to that of plate 10, figures 29 and 29a. The usual form (pl. 3, fig. 19) has the embryonic whorls ochraceous tawny; postembryonic whorls pallid neutral gray axially streaked and faintly spirally lined with deep neutral gray, on the last half whorl the streaks are deep purplish gray; sutural and subsutural bands white; lip and columella callus tilleul buff. Length 18.8 mm., greater diameter 12.2 mm., spire height 10.6 mm.

**ACHATINELLA APEXFULVA APICATA (Newcomb) Pfeiffer**

PLATE 3, FIGURE 14; PLATE 11, FIGURES 2, 3

*Achatinella apicata* (Newcomb) PFEIFFER, Proc. Zool. Soc. London, 1855, p. 210.

*Achatinella apexfulva apicata* (Newcomb) PFEIFFER, Pilsbry and Cooke, Man. Conch., vol. 22, pp 324, 325, 328, pl. 60, figs. 4a, 4c (only), 1914.

There are two specimens of *A. a. apicata* in the type lot. One of them marked "A" by me (pl. 11, fig. 2) is considered the lectotype.

The embryonic whorls are ochraceous buff shading to ochraceous tawny, penultimate whorl pale drab gray axially streaked with mouse gray, last whorl vinaceous buff axially streaked with verona brown, last half whorl streaked with russet, last whorl at the edge of the periphery has a line of light vinaceous buff; lip light vinaceous fawn. Length 20.5 mm., greater diameter 12.8 mm., number of whorls  $6\frac{1}{2}$ .

Distribution, area 92: **Helemano**, Gulick; **Poamoho-Helemano Ridge**, locality 300E, elevation 1,250-1,300 feet, H. Lemke; **Wahiawa**, Gulick (fig. 5a, p. 105). Lectotype, BM.

The usual form in the Gulick collection (pl. 3, fig. 14) has the embryonic whorls ochraceous tawny; first three-fourths postembryonic whorl tilleul buff axially streaked with vinaceous fawn, remaining whorls with ground color of pale pinkish cinnamon darkening on the last whorl to light pinkish cinnamon, and pale pinkish cinnamon on the last half whorl, axially streaked on the penultimate with army brown, benzo brown, and shaded or streaked with pale drab gray, the first half of the last whorl streaked and sparsely lined with brownish drab, last half whorl strongly streaked with army brown or walnut brown, just above the edge of the periphery of the last whorl a white line or band; lip and columella callus vinaceous buff. Length 19.7 mm., greater diameter 12.8 mm., spire height 11.2 mm., number of whorls  $6\frac{3}{4}$ .

On an obese shell with wide axial streaks (pl. 11, fig. 3) the embryonic whorls are ochraceous tawny; ground of the postembryonic whorls pale ochraceous salmon deepening on the last whorl to light ochraceous salmon, and axially streaked or shaded with army brown, fawn, or light drab, on the last whorl above the periphery a faint line of pale ochraceous salmon, base spirally banded with light buff; impressed sutural band russet. Length 19.1 mm., greater diameter 13.3 mm., spire height 10.4 mm.

**ACHATINELLA APEXFULVA APICATA** var. 1

PLATE 3, FIGURE 20; PLATE 11, FIGURES 4-7a

Area 95: **North-South Helemano Ridge**, locality 312-2, elevation 1,550 feet; 312-3, elevation 1,500-1,600 feet, 6 dextral; 312-4, elevation 1,600-1,650 feet; 312-5, elevation 1,650 feet, Meinecke, 1933; 310\*, elevation 1,400-1,450 feet, 1932; 311\*, elevation 1,450-1,500 feet, 1932; 312-2-4\*, 1932, all collected by Meinecke. All the 1932 localities are plotted from memory and may be too low (figs. 5, 5a, p. 105).

The shell is similar to *A. a. apicata* but differs in having the usual form narrower; the usual color pattern finely streaked with grayish

brown instead of widely streaked with reddish brown; sutural band the same color as the rest of the whorl; ground color not as pinkish as some specimens of *A. a. apicata* (pl. 11, fig. 3). The embryonic whorls of the usual form (pl. 3, fig. 20) are worn and are best described from another specimen; postembryonic whorls tilleur buff finely axially streaked with hair brown, benzo brown, fuscous, and a few streaks of natal brown, on the last half whorl the ground color shaded with mouse gray, streaked with fuscous; impressed sutural band wood brown; lip and columella callus vinaceous fawn. Length 19.0 mm., greater diameter 12.0 mm., spire height 10.9 mm., number of whorls  $6\frac{1}{4}$ .

An obese form (pl. 11, fig. 4) has ochraceous tawny embryonic whorls; first fourth postembryonic whorl tawny faintly streaked with ochraceous tawny, last half whorl pale pinkish cinnamon axially streaked with drab gray and cinnamon drab, penultimate whorl tilleur buff axially streaked with hair brown, benzo brown, and natal brown, first half of last whorl tilleur buff, shaded with drab gray, axially streaked with hair brown and natal brown, last half whorl drab axially streaked with tilleur buff, fuscous, and dark vinaceous brown at and below the periphery lined with pale drab gray; impressed sutural band the same as the rest of the whorl. Length 19.4 mm., greater diameter 13.2 mm., spire height 10.3 mm.

A light brownish specimen (pl. 11, fig. 5) resembles *A. a. apicata*, but differs in not having a brown sutural band distinct from the rest of the whorl and in having a color pattern with a shade of brown not found on *A. a. apicata*. The postembryonic whorls are pale ochraceous buff, strongly axially streaked with tawny olive and a few streaks of warm sepia.

Throughout area 96, odd specimens (pl. 11, fig. 6) occur of an entirely different pattern. The shell has the usual embryonic whorls; postembryonic whorls light pinkish cinnamon banded and mottled and lined with chocolate, the bands broken in places by the ground color; lip and columella callus light vinaceous fawn.

One specimen (pl. 11, fig. 7) has the first two postembryonic whorls with the usual color pattern of plate 11, figure 4, and the last half similar to plate 11, figure 6.

Another shell (pl. 11, fig. 7a) looks as if it were diseased, the first fourth postembryonic whorl cinnamon axially streaked with cinnamon buff, the next whorl and three-quarters warm blackish brown faintly streaked with pale drab gray, resembling *A. a. apicata* var. 1, last three-fourths whorl white spirally banded or spotted with tawny and might be taken for a faded color pattern of figure 6.



**ACHATINELLA APEXFULVA APICATA var. 2**

PLATE 3, FIGURE 23; PLATE 11, FIGURES 14-16d

Area 96: **Kawaihalona Gulch**, locality 324, elevation 1,450 feet, 4 dextral 1933; 325, elevation 1,500-1,600 feet, 4 dextral 1933; 326\*, elevation 1,600-1,650 feet, 3 dextral 1932, all collected by Meinecke. Other collectors of *A. a. apicata* var. 2 in Kawaihalona Gulch are Wilder, BBM 50509-50510, Cheatham in Thurston collection, BBM 130851. The material is unlocalized and probably is a mixture of several races (figs. 5, 5a, p. 105).

Very little accurate information is available on the shells of Kawaihalona. From the data on hand it appears that the characteristic pattern is similar to plate 3, figure 23. Embryonic whorls a dark shade of ochraceous buff; first fourth postembryonic whorl tawny axially streaked with ochraceous buff, remaining postembryonic whorls pale pinkish buff darkening to light buff, strongly axially streaked and spirally lined or banded with hair brown or fuscous; impressed sutural band the color of the rest of the whorl; lip and columella callus pale vinaceous fawn. Length 19.2 mm., greater diameter 13.2 mm., spire height 10.7 mm., number of whorls 6+.

A darker banded pattern (pl. 11, fig. 14) has the postembryonic whorls dark vinaceous brown axially streaked and banded and lined with pallid mouse gray changing on the last fourth whorl to tiller buff. The base of this specimen is flattened.

Besides the above patterns, which have been checked by dead specimens collected by Meinecke in area 96, a color pattern (pl. 11, fig. 15) similar to *apicata* var. 1 (pl. 11, fig. 4) is found in locality 326. The embryonic whorls are light buff deepening to warm buff; postembryonic whorls pale vinaceous fawn axially streaked with cinnamon drab and bone brown, last whorl with a line of pale vinaceous fawn above, below, and at the edge of the periphery.

In the Wilder collection, lot BBM 50510 had no locality label on the shells when it came into the Bishop Museum. The lot may be a mixture, for shells with color patterns similar to *A. a. suturafusca* var. 2 (pl. 3, fig. 13) and other patterns are found mixed in with what I suppose may be shells from Kawaihalona, because the color pattern of plate 3, figure 23, occurs in the lot, and because of the position of the lot in the Wilder collection when first received by the Museum. Although the locality data are faulty and should be checked, some peculiar patterns occur in this lot which are worthy of note since they are not recorded from any plotted locality today.

Plate 11, figure 16, is a color pattern similar to plate 11, figure 15, except that it is banded on the last whorl above and below the periphery with a band of pale ochraceous buff which is the ground color. The shell may have a zigzag pattern (pl. 11, fig. 16a), the postembryonic whorl hay's brown or sorghum brown, axially streaked with straight or zigzag streaks of pale mouse gray. An extreme narrow shell (pl. 11, fig. 16b) with a more marked zigzag pattern measures: Length 19.0 mm., greater diameter 11.9 mm., spire height 10.6 mm.; postembryonic whorls warm blackish brown, axially streaked with zigzag lines of warm buff. Another specimen (pl. 11, fig. 16c) shows another form of a narrow shell with a flattened base; postembryonic whorls chestnut faintly axially streaked or splotched with warm buff; impressed sutural band warm buff. Length 18.8 mm., greater diameter 12.0 mm., spire height 10.6 mm.

But by far the most unusual pattern, with the exception of patterns 16b and 16c, is the shell of plate 11, figure 16d. The embryonic whorls are a deep shade of ochraceous buff; postembryonic whorls fawn color sparsely axially streaked with pale ochraceous buff; impressed sutural band fawn color. This color pattern may be a pure race somewhere, possibly in the North Heleman or the South Heleman at a low elevation below area 95. It looks very much like typical *A. a. apicata*.

**ACHATINELLA APEXFULVA PAALAENSIS, new subspecies**

PLATE 3, FIGURE 21; PLATE 12, FIGURE 20

The shell is related to *A. a. apicata* var. 1 but differs in having a blue-gray color pattern instead of a brown one. The holotype (pl. 3, fig. 21) has the embryonic whorls ochraceous tawny; first half postembryonic whorl mikado brown axially streaked with white, remaining whorls white axially streaked with light gull gray, and light neutral gray; impressed sutural band the color of the ground, except on the last half whorl where it is shaded with cinnamon drab; lip and columella callus light vinaceous fawn. Length 18.1 mm., greater diameter 12.1 mm., spire height 9.7 mm., number of whorls 6+.

Distribution, area 106: **North-South Heleman Ridge**, type locality 313-3, elevation 1,600-1,700 feet, 1933; **South Heleman Stream**, locality 301c, elevation 1,350-1,400 feet, 4 dextral, Meinecke, 1933 (figs. 5, 5a, p. 105).

The color pattern in area 106 may be darker (pl. 12, fig. 20) and the form narrower than the holotype; last two and a half postembryonic whorls pale gull gray axially streaked with deep mouse

gray and dark mouse gray, below the periphery a line of dark mouse gray, the entire last whorl faintly lined with a light shade of deep mouse gray; outer margin of the lip vinaceous fawn, inner edge and the columella callus white. Length 18.0 mm., greater diameter 11.8 mm., spire height 9.7 mm.

**ACHATINELLA APEXFULVA PAALAENSIS var. 1**

PLATE 12, FIGURES 21-22*b*

Area 107: **North-South Helemano Ridge**, locality 313-1, elevation 1,700-1,800 feet, 6 dextral 1933; 314-1, elevation 1,650-1,750 feet, 1932, 1933; 315-2, elevation 1,800-1,864 feet, 7 dextral 1933; 315-3, elevation 1,800 feet, 1 dextral 1933; 316-1, elevation 1,750-1,800 feet, 1933, 4 dextral 1934; 316-3, elevation 1,700-1,800 feet, 5 dextral 1933, 3 dextral 1934; 316-1-3, 1932, all Meinecke-collected; **Kawaihalona-Opaaula Ridge**, locality 332\*, elevation 1,700-1,850 feet, Russ, 2 dextral 1931, Meinecke, 1 dextral 1932; **Helemano-Opaaula Ridge**, 334, elevation 1,450 feet, 1932, 1934; 336-1\*, elevation 1,850 feet, 1929; 336-2, elevation 1,800-1,850 feet, 1 dextral 1934, all Meinecke-collected. Also collected by O. H. Emerson, BBM 103977-103982, J. S. Emerson, BBM 102291 (figs. 5, 5*a*, p. 105).

Throughout this region the shells are a mixture of blue-gray forms and pinkish blue-gray or pink color patterns. The usual color pattern and form of the shell on the North-South Helemano Ridge (pl. 12, fig. 21), has the embryonic whorls ochraceous buff; first half of first postembryonic whorl axially streaked with vinaceous cinnamon and pale pinkish buff, next whorl and a half white axially streaked with vinaceous brown, and dark vinaceous brown with a spiral band of dark vinaceous gray on the last half of the penultimate on the upper third of the whorl, last whorl white or pale vinaceous fawn, and heavily streaked with light vinaceous drab, dark vinaceous drab and faintly spirally lined and banded with light quaker drab; lip and columella callus light vinaceous fawn. Length 19.9 mm., greater diameter 12.7 mm., spire height 11.1 mm.

The shell may be bluish gray (pl. 12, fig. 21*a*); last two and a half postembryonic whorls white or a very dilute tint of pallid quaker drab axially streaked with mouse gray and deep quaker drab. A narrow shell and light pink color pattern (pl. 12, fig. 21*b*) has the penultimate whorl axially streaked with white and vinaceous cinnamon, first half of last whorl axially streaked with white and buff pink and a faint band above the periphery of light cinnamon drab, last half of last whorl light russet vinaceous deepening to light brownish drab on the

last fourth of the whorl, axially streaked with a color lighter than the ground and spirally banded and lined with light brownish drab. Length 19.7 mm., greater diameter 12.7 mm., spire height 10.5 mm.

The shape of the usual form and color pattern (pl. 12, fig. 22) of the shell on the Kawaihalona-Opacula Ridge or the Helemano-Opacula Ridge is more elongate and the color pattern darker. The embryonic whorls are ochraceous buff; postembryonic whorls vinaceous pink axially streaked and faintly spirally banded with benzo brown; lip and columella callus light vinaceous fawn. Length 20.0 mm., greater diameter 12.5 mm., spire height 11.3 mm. An obese shell with a light pinkish-gray pattern (pl. 12, fig. 22a) has pale vinaceous fawn postembryonic whorls axially streaked and faintly banded with drab gray or light drab. Length 19.6 mm., greater diameter 13.3 mm., spire height 10.4 mm.

In the lot collected at locality 334 in 1932 by Meinecke a few narrow yellowish-brown shells (pl. 12, fig. 22b) are found. This pattern possibly belongs to a lower race, but until more is known about this color form it will be considered to be *A. a. paalaensis* var. 1. The embryonic whorls are ochraceous buff; postembryonic whorls light pinkish cinnamon axially streaked with light drab, and drab on the first two whorls, last whorl axially streaked with saccardo's umber and snuff brown, on the last two whorls above the periphery a band of white or a dilute tint of pale pinkish buff, below the periphery of the last whorl a line of snuff brown; lip and columella callus light vinaceous fawn. Length 19.6 mm., greater diameter 12.0 mm., spire height 11.4 mm.

**ACHATINELLA APEXFULVA PAALAENSIS** var. 2

PLATE 3, FIGURE 24

Area 109: **Helemano-Opacula Ridge**, locality 337-1, elevation 1,800-1,850 feet, 1934; 337-2, elevation 1,800-1,900 feet, 1934; 337-3, elevation 1,750-1,900 feet, 1934, Meinecke; 337-1-2?, Meinecke, BBM 122320-122321, 1929; 337-1-3?, Meinecke, BBM 122268-122269, 1928, BBM 122362-122368, 1932. Also collected by Wilder, BBM 50513-50517, O. H. Emerson, BBM 103985 (figs. 5, 5a, p. 105).

In area 109 the pink-streaked pattern of *paalaensis* var. 1 becomes dominant over the bluish-gray pattern. The usual form and color pattern (pl. 3, fig. 24) has the usual ochraceous buff embryonic whorls; first half postembryonic whorl axially streaked with ochraceous tawny and pale cinnamon pink, next two whorls pale ochraceous salmon axially streaked with russet vinaceous, last half whorl cameo brown

with a few axial streaks of light vinaceous cinnamon and a faint band of white at the periphery; lip, sutural and subsutural bands light vinaceous fawn. Length 20.0 mm., greater diameter 12.7 mm., spire height 10.7 mm., number of whorls  $6\frac{1}{2}$ .

**ACHATINELLA APEXFULVA KAWAIKI, new subspecies**

PLATE 3, FIGURE 29; PLATE 12, FIGURES 26, 26a

The shell is similar in form to the elongate shell of *A. a. paalaensis* var. 1 (pl. 12, fig. 22b) but has a lighter gray color pattern and usually tends not to have the yellowish embryonic whorls of figure 22b. The holotype (pl. 3, fig. 29) has the first embryonic whorl and a half white, last embryonic whorl and a half pale cinnamon pink; first half postembryonic whorl pale cinnamon pink axially streaked with light pinkish cinnamon, next two postembryonic whorls pale drab gray axially streaked with light cinnamon drab, last half whorl tinted with wood brown, last whorl with a line of white below the impressed sutural band, and a band of white below the periphery; impressed sutural band pale pinkish buff; lip and columella callus vinaceous buff. Length 19.9 mm., greater diameter 12.2 mm., spire height 11.6 mm., number of whorls  $6\frac{5}{8}$ .

Distribution, area 99: **Kawaiiki-Kawainui Ridge**, locality 350, elevation 1,550-1,600 feet, 1 dextral; 351, elevation 1,600 feet, 2 dextral 1933; the type lot collected in 1913 from the same ridge was localized from the 1933 material, all Meinecke-collected. Also collected by Wilder, BBM 50506-50507, Thurston, BBM 130892 (figs. 5, 5a, p. 105).

An extreme obese shell (pl. 12, fig. 26) has the embryonic whorls light buff; postembryonic whorls pale drab gray faintly axially streaked with drab gray, last whorl lined above and below the periphery with white; impressed sutural band white; lip and columella callus light pinkish cinnamon. Length 20.1 mm., greater diameter 13.7 mm., spire height 11.1 mm.

The shell may be more conspicuously banded (pl. 12, fig. 26a) and have darker embryonic whorls; embryonic whorls warm buff; last two and a half postembryonic whorls drab gray, axially streaked on the penultimate with light cinnamon drab, last whorl streaked with drab and light drab, last two and a half whorls above the periphery have a band of tilleul buff, below the periphery three bands of tilleul buff; lip and columella callus vinaceous buff. Length 19.0 mm., greater diameter 12.1 mm., spire height 10.8 mm. This form resembles *A. a. paalaensis* var. 1 (pl. 12, fig. 22b).



GROUP OF *A. a. aloha* PILSBRY AND COOKE**ACHATINELLA APEXFULVA ALOHA** Pilsbry and Cooke

PLATE 2, FIGURE 31; PLATE 12, FIGURES 1-2a

*Achatinella apexfulva aloha* PILSBRY and COOKE, Man. Conch., vol. 22, p. 330, pl. 60, figs. 15-15a (only), 1914.

To quote from Pilsbry and Cooke:

The shell is dextral, rather small and light, often perforate; white, with *unequal spiral bands of pale cinnamon pink* on the penultimate and last whorls, deepening to brownish vinaceous or orange-cinnamon behind the lip, where they usually become confluent. The *embryonic whorls and a broad band below the suture are white*. Peristome moderately thickened within, light purplish vinaceous, the columellar fold paler.

Length 18.5, diam. 12.7 mm.;  $6\frac{1}{3}$  whorls.Length 19.2, diam. 11.9 mm.;  $6\frac{1}{2}$  whorls.

Crest of the division ridge between the two branches of the Kaukinahua [Kaukonahua] stream, above the Waliawa head-gates cabin, the colony extending to within  $\frac{3}{4}$  mile of main ridge; on mokihaia [mokihana?], pua [*Osmanthus*], maile [*Alyria*], and alani [*Pelea*]. Cotypes in collections A.N.S.P. and Bishop Mus., from No. 3813 Irwin Spalding Coll.

By its cleanly-defined pinkish bands, absence of streaks and white embryo, this snail is well distinguished from other forms of *A. apexfulva*. It is very constant in a large series collected by Mr. Spalding, except for a mutation which occurs in the same colony. This is illustrated in pl. 60, fig. 16, and differs from the normal *A. a. aloha* only by having the bands chocolate-black.

*A. a. aloha* is always dextral. It is plentiful in a limited locality on one ridge, which is isolated by perennial streams on both sides, and *mauka* (toward the mountains) is shut in by the precipitous side of the main Koolau Range.

Distribution, area 100?: **Kaukonahua**, Wilder, BBM 50561; **North Kaukonahua Stream**, Thurston, BBM 130740. Lectotype BBM (pl. 12, fig. 1). Pilsbry and Cooke plot this locality in the region of area 100?. This locality has not been collected in recent years. Since their information was obtained from Spalding, I believe that the Wilder and Thurston shells can be plotted as coming from the same place because these men either collected together or told each other about their localities so that they could visit them separately (fig. 5a, p. 105).

The usual form and color pattern (pl. 2, fig. 31) on 87 percent of the shells in the Wilder collection has the first postembryonic whorl and penultimate white, penultimate banded just above the edge of the periphery with pale ochraceous salmon, last whorl pale ochraceous salmon with a few faint broken lines of white, sutural and subsutural bands white; lip tinged with pale grayish vinaceous; columella callus white. Length 19.2 mm., greater diameter 13.2 mm., spire height 9.6 mm.

A slightly more obese form (pl. 12, fig. 2) has a similar pattern to plate 2, figure 31 except that it is banded on the last whorl with white like the lectotype. Length 19.2 mm., greater diameter 13.5 mm., spire height 9.5 mm. A narrow specimen (pl. 12, fig. 2a) shows the white form of the shell occurring on 13 percent of the shells; entire shell white, last whorl with lines slightly darker than the ground color; outer margin of the lip ochraceous tawny, remainder of lip and columella callus white. Length 18.9 mm., greater diameter 11.8 mm., spire height 10.0 mm.

**ACHATINELLA APEXFULVA ALOHA var. 1**

PLATE 2, FIGURE 32; PLATE 12, FIGURES 3, 3a

*Achatinella apexfulva aloha* PILSBRY and COOKE, Man. Conch., vol. 22, p. 330, pl. 60, fig. 16 (only), 1914.

Area 100?: **Kaukonahua**, Wilder, BBM 50559-50560; **North Kaukonahua Stream**, Thurston, BBM 103741 (fig. 5a, p. 105). This form of *aloha* has an entirely different color pattern from that of typical *aloha* but is found as a rare pattern mixed with typical *aloha*. It is possible that this is a separate race occurring above or below the typical *aloha* area. Future collecting will have to determine this point. Pilsbry considered this variety to be a mutation of *aloha*. (See above description of *A. a. aloha*, p. 160).

The usual form and color pattern (pl. 2, fig. 32) has white embryonic whorls; postembryonic whorls above the periphery white, banded on the last two and a half whorls just above the periphery with claret brown, lined on the last half of the penultimate and the first half of the last whorl below the white subsutural band with a line of clay color, which widens and darkens to a band of claret brown on the last half whorl, below this a line of claret brown on the last whorl, peripheral band on last whorl white, with a central line of claret brown on the last half whorl, base claret brown lined with white within and just without the aperture; impressed sutural band white; lip and columella callus light vinaceous fawn. Length 18.9 mm., greater diameter 13.1 mm., spire height 9.9 mm., number of whorls  $6\frac{1}{2}$ .

This form may be more heavily banded with claret brown so that the last whorl is almost solid claret brown and lined or banded with white.

The lightest color pattern and elongate form (pl. 12, fig. 3) is a white shell banded just above the edge of the periphery with two bands of claret brown on the last two whorls, on the last whorl a

central line of claret brown, between the two bands, last whorl at and below the periphery white, banded and lined with claret brown; lip and columella callus light vinaceous fawn. Length 20.8 mm., greater diameter 12.8 mm., spire height 11.2 mm.

On 6 percent of the Wilder shells a gray lined color pattern occurs (pl. 12, fig. 3a); embryonic whorls white; postembryonic whorls white faintly banded above the edge of the periphery with a band made up of lines of pale drab gray, which are so faint as to be almost white on the penultimate, on the last half whorl the lines darkening to hair brown and the ground color of the band shaded with pale olive gray, the peripheral band of white shaded or faintly axially streaked with pale olive gray and outlined above by two lines and below by three lines of bone brown which become a single band on the last half of the whorl, base white shaded with pale olive gray and spirally lined with army brown.

**ACHATINELLA APEXFULVA ROSEIPICTA**, new subspecies

PLATE 3, FIGURE 7; PLATE 12, FIGURES 4-4b

The form of the shell closely resembles that of *A. a. beata*. The color patterns, however, tend toward pastel shades of pink and are closer to those of *A. a. aloha*. The race seems to be intermediate between *A. a. beata* and *A. a. aloha*. The embryonic whorls of the holotype (pl. 3, fig 7) are pale pinkish cinnamon; postembryonic whorls below the white impressed sutural and wide subsutural bands are walnut brown faintly axially streaked or tinted with white and a faint line of burnt umber just below the subsutural band, the ground shading on the last whorl to vinaceous, russet, and kaiser brown on the last half whorl with a faint band of white at the edge of the periphery, which fades out on the last half whorl; lip and columella callus pale grayish vinaceous. Length 19.5 mm., greater diameter 13.0 mm., spire height 10.0 mm., number of whorls 6½.

Distribution, area 102: **North Kaukonahua-Poamoho Ridge**, type locality 286, elevation 1,950 feet, 1933, 1936; also locality 285-3, elevation 1,850 feet, 1933; 285-4, elevation 1,750-1,900 feet, 1936; all collected by Meinecke (figs. 5, 5a, p. 105). Also collected by O. H. Emerson, BBM 103984, on "Spurs north-east of head-gates, Kaukonahua," 1917. The head gates are probably in the North Kaukonahua. Also collected by Wilder, BBM 50563, but the shells have no original label and are marked Poamoho? by C. M. Cooke, Jr., who surmised the locality to be somewhere in that region from the arrangement of this lot in the Wilder collection.

A lighter color pattern (pl. 12, fig. 4) occurs on 37 percent of the shells in area 102; the last two postembryonic whorls and a half pale congo pink faintly lined and banded with vinaceous pink, edge of the periphery of the last whorl banded with a band of white tinted with a very dilute tint of pale congo pink or a dilute pinkish tint of pale vinaceous fawn, base vinaceous pink; subsutural and impressed sutural band white. Length 19.8 mm., greater diameter 12.0 mm., spire height 11.6 mm. Forty-one percent of the shells have the color pattern of the holotype.

Sixteen percent have a pinkish gray or gray color pattern shown by an obese shell (pl. 12, fig. 4a), which has a concave spire, the first two postembryonic whorls white, last whorl and a half below the white sutural and subsutural bands are a very dilute tint of pale grayish vinaceous spirally lined with pale grayish vinaceous, in the umbilical region a patch of honey yellow. Length 19.7 mm., greater diameter 13.8 mm., spire height 9.7 mm.

Six percent have a white color pattern (pl. 12, fig. 4b); which has a spire straight in outline; embryonic whorls pale cinnamon pink shading to white on the first half postembryonic whorl, the remaining whorls white, in the umbilical region a dot or small patch of honey yellow.

**ACHATINELLA APEXFULVA ROSEIPICTA var. 1**

PLATE 3, FIGURE 8; PLATE 12, FIGURES 5-6

Area 103: **North Kaukonahua-Poamoho Ridge**, locality 289-1a, elevation 2,000-2,050 feet, 1933; 287-1-2, elevation 1,900 feet, 1933; 287-1, elevation 1,900 feet, 8 dextral 1936; 287-2, elevation 1,900 feet, 2 dextral 1936; 287-3, elevation 1,900-1,950 feet, 1936; 288, elevation 1,900-2,068 feet, 1933; all collected by Meinecke (figs. 5, 5a, p. 105).

This variety is intermediate between *A. a. aloha* and *A. a. roseipicta*. The banding resembles *aloha* but the color is much darker and is closer to *roseipicta*. The usual form (pl. 3, fig. 8) and a color pattern, found on 17 percent of the shells, has the embryonic whorls white; postembryonic whorls white, banded and lined with avellaneous, peripheral band white, outlined above and below by bands of cinnamon rufous, base cinnamon rufous, banded with tilleul buff and a band of white; impressed sutural and subsutural bands white; lip and columella callus light vinaceous fawn. Length 19.1 mm., greater diameter 13.0 mm., spire height 9.8 mm., number of whorls 6 $\frac{1}{4}$ .

Eight percent of the shells have a reddish-brown color pattern (pl. 3, fig. 7).

The usual pink-lined color pattern on 67 percent of the shells and the obese form of the shell (pl. 12, fig. 5), has the first two postembryonic whorls tiller buff below the white sutural and subsutural bands, last whorl vinaceous buff, banded above and at the periphery with white, below the periphery lined with fawn color. Length 19.4 mm., greater diameter 14.0 mm., spire height 9.6 mm. The usual narrow form of the shell (pl. 12, fig. 5a) measures: Length 19.6 mm., greater diameter 12.7 mm., spire height 10.2 mm.; has an extremely light pink lined pattern; postembryonic whorls white faintly lined with a very dilute tint of seashell pink darkening on the last half whorl to buff pink lines or bands.

In locality 287-2 a dark gray color pattern occurs on two specimens. The color pattern (pl. 12, fig. 6) is similar to that of *A. a. poamohoensis* except that the gray ground color is broken up with light lines and bands. The embryonic whorls are pale pinkish buff; postembryonic whorls below the white sutural and subsutural bands pallid mouse gray spirally lined with benzo brown, peripheral band on the first fourth of the last whorl pale smoke gray, last three-fourths whorl bone brown or natal brown, lined and banded with light vinaceous fawn. One shell, or 2 percent, has a white pattern similar to that of plate 12, figure 4b. Another shell from locality 289-1a is black lined and similar to plate 12, figure 3a.

**ACHATINELLA APEXFULVA ROSEIPICTA var. 2**

PLATE 3, FIGURE 18; PLATE 12, FIGURES 9-12a

Area 105: **Central Poamoho Stream**, locality 280F-1, elevation 1,550 feet, 5 dextral 1933; 280F-2, elevation 1,600 feet, 1933, 1936; 280F-3, elevation 1,600-1,650 feet, 4 dextral 1933, Meinecke; **Poamoho-Heleman Ridge**, 306-4, elevation 1,700-1,950 feet, Welch, 3 dextral 1935; 307-1a-1b, elevation 1,800-1,850 feet, Meinecke, 1917, 5 dextral 1935; 307-1, elevation 1,800-1,850 feet, C. W. Isle, 1 dextral 1935, Welch, 1 dextral 1935; 307-1-2, elevation 1,800-1,965 feet, Meinecke, 5 dextral 1934; 307-3, elevation 1,950 feet, Lemke, 1934; 307-3-308-1, elevation 1,850-1,950 feet, Meinecke, 1934; 308-1, elevation 1,850-1,900 feet, Welch, 2 dextral 1935, Russ, 10 dextral 1931, Russ, BBM 134206, 120037, 1932; 308-2, elevation 1,850-1,900 feet, Welch, 1 dextral 1935, C. W. Isle, 1 dextral 1935; also collected by Lemke above 307-3, BBM 10444, 1934 (figs. 5, 5a, p. 105).



The usual color pattern (pl. 3, fig. 18) is lighter and not so sharply banded as that of typical *beata*. The form resembles *roseipicta* var. 1 in shape and color pattern but differs in shade and range of the color patterns. The race is intermediate between *A. a. roseipicta* and *A. a. beata*. The embryonic whorls are cartridge buff; first two postembryonic whorls white, penultimate whorl banded in the center of the whorl with a band of vinaceous fawn, last whorl below the white sutural and subsutural bands pale vinaceous fawn or a dilute shade of pale vinaceous fawn, banded with vinaceous fawn, in the umbilical region a band of white; lip a faint tint of pale vinaceous fawn, columella callus white. Length 20.0 mm., greater diameter 13.1 mm., spire height 11.1 mm. The usual form is not determined by measurement because of insufficient material. This shell is probably near the usual form.

An obese shell and light color pattern (pl. 12, fig. 9) has white postembryonic whorls banded on the last whorl above the periphery with a band of light vinaceous fawn darkening to vinaceous fawn on the last half whorl, last half whorl below the periphery faintly shaded or lined with a dilute tint of vinaceous fawn. Length 19.8 mm., greater diameter 13.5 mm., spire height 10.0 mm. The shell may have pure white embryonic whorls.

In the higher localities of 307-3 and 308-1 a form (pl. 12, fig. 10) occurs which resembles in color *A. a. aloha* (pl. 12, fig. 2) except that the bands are a darker shade and a different hue. The shell of figure 10 also shows an elongate form; postembryonic whorls white, lined just above the edge of the periphery with two bands of pinkish buff, a very dilute shade on the first whorl and darkening to a stronger shade on the next two whorls, the lower band being pinkish cinnamon on the last whorl, last whorl below the periphery banded or lined with pinkish cinnamon the ground color pale pinkish cinnamon.

A dark color pattern (pl. 12, fig. 11) has a grayish-pink color; first half of the last postembryonic whorl below the white sutural and subsutural bands ecru drab, tinted, faintly lined, and finely axially streaked with light vinaceous fawn, last half whorl cinnamon drab faintly tinted or finely streaked with benzo brown, at the edge of the periphery a band of white, which fades out on the last half whorl.

In locality 308-2 and in other localities at the upper limit of area 106 a gray pattern (pl. 12, fig. 12) occurs which resembles *aloha* var. 1 (pl. 12, fig. 3a), but does not have its obese appearance. The embryonic whorls are pale pinkish buff; postembryonic whorls white, banded

on the last whorl and a half with pale drab gray below the white sutural band, above the white peripheral band banded with hair brown, below the periphery base banded with hair brown and white; lip and columella callus vinaceous fawn.

Lemke found a pink color pattern (pl. 12, fig. 12a) which looks like *A. a. roseipicta*, the last whorl and a half vinaceous fawn, finely axially streaked with light vinaceous fawn, on the last whorl at the periphery a band of pale drab gray which fades out on the last fourth whorl, base lined with light vinaceous fawn, a band of white in the umbilical region.

**ACHATINELLA APEXFULVA POAMOHENSIS, new subspecies**

PLATE 3, FIGURES 5, 6; PLATE 12, FIGURES 7-8

The shell is similar in form to the higher race of *A. a. roseipicta*, but differs in having a gray instead of a pink color pattern. The embryonic whorls of the holotype (pl. 3, fig. 6) are white; post-embryonic whorls white faintly banded on the penultimate with a central band of pale drab gray, last whorl pale drab gray faintly spirally lined with white; lip and columella callus pale vinaceous fawn. Length 19.7 mm., greater diameter 12.8 mm., spire height 9.6 mm., number of whorls 6½.

Distribution, area 101: **North Kaukonahua-Poamoho Ridge**, type locality 284-2, elevation 1,700-1,800 feet; also locality 283-3, elevation 1,750 feet, 5 dextral, 1 sinistral; 283-1, elevation 1,650-1,750 feet, 6 dextral; 283-4, elevation 1,600-1,650 feet, 4 dextral; 284-1, elevation 1,550-1,600 feet, 4 dextral; 285-1, elevation 1,750-1,800 feet, 13 dextral; 285-2, elevation 1,750-1,850 feet, 1 dextral; all collected by Meinecke, 1933 (figs. 5, 5a, p. 105).

The usual form of the shell and the dark color pattern (pl. 12, fig. 7) has the embryonic and first postembryonic whorls light buff, penultimate whorl below the white sutural and subsutural bands pale drab gray finely and faintly spirally lined and finely axially streaked with benzo brown, ground of last whorl drab gray, deepening to light drab on the last whorl, finely axially streaked with benzo brown, below the periphery the color shading to saccardo's umber faintly lined with benzo brown, in the umbilical region a patch of cream color; lip and columella callus tilleul buff, outer margin of lip avellaneous. Length 19.3 mm., greater diameter 12.7 mm., spire height 10.8 mm.

The usual yellow pattern and the obese form of the shell (pl. 12, fig. 7a) measures: Length 19.1 mm., greater diameter 13.0 mm., spire height 9.5 mm.; embryonic and postembryonic whorls light buff,

spirally banded above the periphery on the first half of the last postembryonic whorl with a faint band of drab gray and a line of cinnamon buff, below the periphery lined with pinkish buff, last half whorl lined, banded, or tinged with pale drab gray; impressed sutural band the color of the ground.

A darker yellow color pattern and elongate shell (pl. 3, fig. 5) has the embryonic whorls pale pinkish buff; postembryonic whorls warm buff, last whorl, below the subsutural band of warm buff, drab gray, and below this, just above the edge of the periphery, a band of warm buff, which fades out on the last half whorl, base drab faintly axially streaked or tinted with warm buff; impressed sutural band pale cinnamon pink; lip and columella callus pale vinaceous fawn. Length 18.7 mm., greater diameter 12.0 mm., spire height 10.4 mm.

An exceedingly dark specimen (pl. 12, fig. 8) is found in locality 283-1; penultimate whorl light drab shading into rood's brown on the last whorl; impressed sutural band pale pinkish buff; subsutural band shading from pale pinkish buff to light buff on the last whorl, on the last half whorl narrowing to a line and fading out.

Below locality 284-2 in area 101 the shells have a yellow ground color, and no shells with white sutural and subsutural bands are present. In locality 284-2 only 6 shells out of 34 have a yellow ground color. In localities 285-1 and 285-2 the impressed sutural and subsutural bands are white, and pinkish gray and white color patterns occur, so that this region appears to be intermediate between *A. a. roscipicta* and *A. a. poamohoensis*.

#### ACHATINELLA APEXFULVA CERVIXNIVEA Pilsbry and Cooke

PLATE 3, FIGURE 15; PLATE 11, FIGURES 8-10

*Achatinella apexfulva cervixnivea* pattern PILSBRY and COOKE, Man. Conch., vol. 22, pp. 322, 328, pl. 60, figs. 8-8a (only), 1914.

The lectotype of *A. a. cervixnivea* is selected by Pilsbry and myself from the figured cotypes (pl. 60, fig. 8) and reproduced in this paper on plate 11, figure 8. The embryonic whorls are buckthorn brown; postembryonic whorls, below the broad white sutural and subsutural bands, dark quaker drab or deep quaker drab, below the periphery of the last whorl the ground is pale mouse gray, spirally banded, lined, and axially streaked with quaker drab; lip and columella callus light vinaceous fawn. Length 20.0 mm., greater diameter 13.6 mm., spire height 10.0 mm., number of whorls 6 $\frac{1}{4}$ .

Distribution, area 93: **Poamoho-Helemano Ridge**, locality 300-4\*, elevation 1,500-1,550 feet, Russ, 1932; 300-5, elevation 1,650 feet.

1 sinistral 1933; 300-6, elevation 1,650-1,700 feet, 1917, 6 dextral 1932, 3 sinistral 1934; 300-7, elevation 1,500-1,700 feet, 4 dextral 1934; 300-8, elevation 1,550-1,700 feet, 4 dextral 1933, 1 dextral 1934; 301-1-2\*, elevation 1,650 feet, 9 sinistral 1932; 300-6-301-2\*, elevation 1,650 feet, 1916, all collected by Meinecke; 300-10, elevation 1,550-1,600 feet, Russ, 4 dextral 1933; 301-1, elevation 1,650 feet, H. B. Baker and Welch, 3 dextral and 6 sinistral 1935; 301-2, elevation 1,650 feet, H. B. Baker and Welch, 1 sinistral 1935. Also collected by Wilder, BBM 50631, 50566 (figs. 5, 5a, p. 105).

The usual form and color pattern (pl. 3, fig. 15) has the embryonic whorls clay color, first fourth postembryonic whorl pale pinkish buff axially streaked or tinged with cinnamon buff, next half whorl pallid quaker drab axially streaked and banded, below the white sutural and subsutural bands, with a band of deep quaker drab, last whorl and a half above the periphery and below the subsutural band vinaceous slate deepening on the last half whorl to dark purple drab, just above the edge of the periphery and all below, ground pale ecru drab finely lined and faintly streaked with deep quaker drab, on the last half of the whorl streaks and lines dark purple drab, in the umbilical region a patch of pale pinkish buff; lip and columella callus light vinaceous fawn. Length 18.8 mm., greater diameter 12.8 mm., spire height 9.8 mm., number of whorls 6.

A light color pattern (pl. 11, fig. 9), has the last two postembryonic whorls, below the white sutural and subsutural bands, pale vinaceous fawn shading to light vinaceous fawn on the last half whorl, spirally banded and faintly axially streaked with ecru drab, on the last half whorl bands and streaks brownish drab, in the umbilical region a band of pale pinkish buff.

The usual form of a sinistral shell (pl. 11, fig. 9a) has a color pattern similar to that of plate 3, figure 15, except that the embryonic whorls in this specimen are warm buff. Length 18.7 mm., greater diameter 12.0 mm., spire height 10.0 mm.

In locality 300-4 the usual pattern has a more pinkish ground than the typical pattern. Among these pinkish gray shells two extremely light pink forms are found. One of these (pl. 11, fig. 10) shows an obese shell; postembryonic whorls with a band of pecan brown below the white sutural and subsutural bands, below which the ground is buff pink streaked and lined on the last whorl with pecan brown; lip and columella callus pale vinaceous pink. Length 19.3 mm., greater diameter 13.6 mm., spire height 10.2 mm.

From the data on hand *cervixnivea* runs from pinkish forms at a low elevation to dominantly light gray shells. At the upper end of

area 93 near area 94 *beata*-like forms and the black forms of *beata* var. 1 are found mixed with *A. a. cerviniviva*.

**ACHATINELLA APEXFULVA BEATA** Pilsbry and Cooke

PLATE 3, FIGURE 17; PLATE 12, FIGURES 13-16

*Achatinella apexfulva beata* PILSBRY and COOKE, Man. Conch., vol. 22, p. 329, pl. 60, figs. 17a-17c; pl. 55, fig. 5 (only), 1914.

*Achatinella apicata* var. *alba* SYKES, Fauna Hawaiiensis, p. 299, 1900. Not *Achatinella alba* Nuttall in Jay's Catalogue, ed. 3, p. 58, 1839 (name only), which is *Achatinella lorata* Férussac.

*Achatinella apexfulva alba* SYKES, Pilsbry and Cooke, Man. Conch., vol. 22, p. 324, 1914.

The shell of Pilsbry's plate 60, figure 17a, reproduced here on plate 12, figure 13, is considered the lectotype. The embryonic whorls are cream color; postembryonic whorls, below the white sutural and subsutural bands, with a band of liver brown, below which is a band of white or seashell pink, last whorl below the white sutural and subsutural bands seashell pink, banded above, at the edge and below the periphery with livid brown, below the periphery the bands faintly axially streaked with seashell pink, in the umbilical region a patch of naples yellow; lip pale vinaceous fawn, columella callus white. Length 19.8 mm., greater diameter 13.0 mm., spire height 11.0 mm., number of whorls 6 $\frac{5}{8}$ . The pattern is dominantly a banded one, and the streaks are faint or not prominent.

Distribution, area 104: **Central Poamoho-Central Poamoho North Branch Ridge**, locality 280L-6, elevation 1,850-1,950 feet, Meinecke, 1933; 280L-7, elevation 1,900 feet, Meinecke, 3 dextral 1933; 280L-9, elevation 1,850 feet, Russ, 1934; **Poamoho-Helemano Ridge**, locality 303, elevation 1,700-1,800 feet, Meinecke, 1934, Russ 1934; 304, elevation 1,800-1,900 feet, Meinecke, 1 dextral 1933, 1 dextral 1934, Welch, 1935; 305, elevation 1,850-2,300 feet, Meinecke, 2 dextral 1933, Welch, 4 dextral 1935; 306-1, elevation 1,850-2,000 feet, Meinecke, 7 dextral 1933; 306-3, elevation 1,750-1,850 feet, 1 sinistral 1934; also 302-304?, BBM 122106, 1916; 305-306-2?, BBM 122112-122113, 1932, less localized Meinecke material plotted from memory; **South Helemano Stream**, locality 300H, elevation 1,500-1,600 feet, Meinecke, 1 dextral 1934; 300G, elevation 1,600-1,750 feet, Meinecke, 6 dextral 1934; **North-South Helemano Ridge**, locality 317, elevation 1,750-1,950 feet, Meinecke, 8 dextral 1934. Other collectors of *A. a. beata* probably from area 104 are Thurston, BBM 130772, Wilder, BBM 50633, Lemke, and others (figs. 5, 5a, p. 105).



The usual form and color pattern (pl. 3, fig. 17) has the embryonic whorls warm buff; first half postembryonic whorl warm buff, last half white with a central band of clay color, last two whorls above the periphery white with a central band of hazel shading into kaiser brown on the last whorl, last whorl below the kaiser brown peripheral band Naples yellow banded with kaiser brown; lip pale vinaceous fawn, columella callus white. Length 19.8 mm., greater diameter 12.8 mm., spire height 10.3 mm.

The lightest color pattern and obese form (pl. 12, fig. 15) has the embryonic whorls light buff; postembryonic whorls white, last whorl above the periphery banded with light pinkish cinnamon, below the edge of the periphery pale pinkish buff faintly banded on the last half whorl at the edge of the periphery and about the base with light vinaceous fawn; lip and columella callus light grayish vinaceous. Length 19.3 mm., greater diameter 13.6 mm., spire height 9.1 mm.

The dark banded color pattern and narrow form (pl. 12, fig. 14) has the first two postembryonic whorls white, banded about the middle of the whorl above the periphery with a band darkening from light pinkish cinnamon on the first postembryonic whorl to pecan brown on the penultimate and last whorl; sutural and subsutural bands white, on the last whorl the white supraperipheral band is shaded with seashell pink, the peripheral band is walnut brown deepening to burnt umber on the last half of the whorl, subperipheral band light vinaceous cinnamon fading out on the last half whorl, remainder of base, except for a patch of pale pinkish buff in the umbilical region, burnt umber faintly lined and axially streaked with light vinaceous cinnamon. Length 20.0 mm., greater diameter 12.3 mm., spire height 11.2 mm.

The color pattern (pl. 12, fig. 16) is similar to plate 3, figure 17, except that the embryonic whorls have a more snow-white ground, and the last whorl below the periphery is massicot yellow faintly banded and axially streaked with fawn color, last fourth whorl streaked with army brown.

The holotype of *A. a. alba* Sykes in the British Museum is a white shell similar to the white color forms of *A. a. beata* and which was collected by Perkins in Kawaihoa. *A. a. beata* would have to be put in the synonymy of *A. alba* if the name *alba* were not already pre-occupied. The name *alba* was used by Nuttall, in Jay's Catalogue, and placed in the synonymy of *A. pallida* Nuttall by Reeve (Conch. Icon., vol. 6, pl. 1, species 2, 1850). No white shells similar to *A. a. beata* have been taken in Kawaihoa proper. Mr. Sykes' shell may have

come from the Helemano-Opaaula Ridge, which is the division ridge between the districts of Paala and Kawaihoa. This ridge is the most northern ridge known to contain white *beata*-like shells.

**ACHATINELLA APEXFULVA BEATA var. 1**

PLATE 3, FIGURE 16; PLATE II, FIGURES 11-13

*Achatinella apexfulva beata* PILSBRY and COOKE, Man. Conch., vol. 22, p. 329, pl. 60, fig. 17 (only), 1914.

Area 94: **Poamoho-Helemano Ridge**, locality 302, elevation 1,750 feet, Meinecke, 1916, 1932, Russ, 2 dextral 1933; 302-291-5, elevation 1,750-1,802 feet, Baker and Welch, 2 dextral 1935; **North-Central Poamoho Ridge**, locality 291-3-5\*, elevation 1,650-1,802 feet, 1916-1917, 1932; 291-5, elevation 1,750-1,802 feet, 4 dextral 1934, all Meinecke localities. Also collected by Wilder, BBM 50568-50569, and others.

Area 94-94a?: **North-Central Poamoho Ridge**, locality 291-2?, elevation 1,600-1,700 feet, 6 dextral 1932; 291-3?, elevation 1,650-1,700 feet, 12 dextral 1926; 291-2-302?, elevation 1,600-1,800 feet, 1914, all Meinecke-collected. The shells in this area contain a mixture of color patterns of typical *A. a. cervixnivea* and *beata* var. 1. All the localities are plotted from memory and are of wide extent. Probably if more localized collecting were done in area 94a, the lower portion of the ridge might contain only *cervixnivea* while the upper portion of area 94 might contain a dominance of the dark color pattern of *beata* var. 1 (figs. 5, 5a, p. 105).

Pilsbry also considered this race a form of *beata*; actually it is a distinct race existing between *beata* and *cervixnivea* with a color pattern distinct from both. However, this form is so close to the typical *apexfulva* that it is almost impossible to tell the difference between the forms. Typical *apexfulva* usually has forms with the last whorl a light yellowish color and banded, lined, and axially streaked with chocolate or black, while *cervixnivea* var. 1 usually has a solid color or patterns intermediate with typical *cervixnivea* or *beata*.

The usual form (pl. 3, fig. 16) from locality 291-3-5 measures: Length 19.4 mm., greater diameter 13.4 mm., spire height 10.3 mm.; the color pattern is a little lighter than usual; embryonic whorls light buff; last two and a half postembryonic whorls chocolate, tinted or lightened with streaks of mahogany red; impressed sutural band warm buff, shaded on the lower half of the band on the last whorl with russet; lip and columella callus white.

A more usual color pattern and the usual form in the Wilder collection (pl. 11, fig. 12) has the last two whorls maroon; impressed sutural band mahogany red, the upper portion of which is lined or edged with pale pinkish buff; lip and columella callus pale vinaceous fawn. Length 19.7 mm., greater diameter 12.8 mm., spire height 10.8 mm. In a lot of 69 shells, 11 percent have white sutural bands similar to those of plate 11, figure 11. The postembryonic whorls on this specimen are particularly dark, being seal brown.

One or two specimens in area 94 have a yellowish color pattern (pl. 11, fig. 13), the embryonic whorls warm buff; first half post-embryonic whorl warm buff lightly axially streaked with ochraceous tawny, on the penultimate and last whorl above the periphery, the upper third of the whorl, including the impressed sutural and sub-sutural bands, amber brown faintly axially streaked with pale orange yellow, below which the middle third of the whorl has a band of dusky brown which is faint on the early whorls and does not really start until the second half of the penultimate, just above the edge of the periphery a band of pale orange yellow, tinted with amber brown, which becomes narrower on the last half of the whorl, below the periphery dusky brown faintly tinted or streaked with pale orange yellow, in the umbilical region a band of mars yellow.

**ACHATINELLA APEXFULVA BEATA var. 2**

PLATE 3, FIGURE 22; PLATE 12, FIGURES 17, 18

Area 108: **North-South Heleman Ridge**, locality 318, elevation 1,800-1,900 feet, 1934; 318a, elevation 1,850-1,950 feet, 1934; 319, elevation 1,850-1,900 feet, 5 dextral 1934; 319a, elevation 1,950-2,000 feet, Meinecke, 1 dextral 1934 (figs. 5, 5a, p. 105).

In area 108 the shells are dominantly white color forms mixed with *beata* color patterns. The usual form of the shell (pl. 3, fig. 22) has the embryonic whorls a dilute shade of light buff; remainder of the shell white except for about 3.5 mm. behind the edge of the lip, where the ground is tinged with naples yellow; lip and columella callus white. Length 19.4 mm., greater diameter 12.7 mm., spire height 11.0 mm.

An extremely obese shell (pl. 12, fig. 17) is pure white; the embryonic whorls are worn and lack the shell nacre; the lip and columella callus white, outer margin of the lip clay color. Length 19.2 mm., greater diameter 13.5 mm., spire height 9.8 mm. A narrow shell (pl. 12, fig. 18) shows the usual light *beata* pattern; postembryonic whorls white, last postembryonic whorl above the periphery with a

band of buff pink deepening to cacao brown on the last half of the whorl, last whorl below the periphery white on the first half of the whorl, last half banded at the edge of the periphery and on the base with cacao brown, subperipheral band white tinged with vinaceous pink. Length 19.7 mm., greater diameter 12.7 mm., spire height 11.2.

**ACHATINELLA APEXFULVA BEATA var. 3**

PLATE 3, FIGURE 25; PLATE 12, FIGURE 19-19b

Area 110: **Heleman-Opaule Ridge**, locality 337-4, elevation 1,900-2,000 feet, 1934; 338, elevation 1,950-2,000 feet, Meinecke, 1934; also less localized Meinecke material plotted from memory, locality 338-339-1?, BBM 128329-128333, 122335-122336, 1929; 339-1a\*, elevation 1,950-2,000 feet, 1929; 338?, BBM 122267, 1928 (figs. 5, 5a, p. 105).

This race differs from *A. a. beata* in usually having lighter pink color patterns and a different range of color patterns. The characteristic pattern of this area (pl. 3, fig. 25) has the embryonic whorls cream buff; first two postembryonic whorls white, first half of the last whorl white faintly shaded with a very dilute color of pale grayish vinaceous, lightly banded with light russet vinaceous, last half whorl vinaceous brown, faintly lined or banded and axially streaked with light russet vinaceous and banded with white in the umbilical region; lip and columella callus light grayish vinaceous. Length 19.6 mm., greater diameter 13.5 mm., spire height 10.3 mm. The aboral surface of this shell is figured in order to show the abrupt change of coloration from white to a dark almost solid pinkish color on the last half whorl. This pattern is found only in area 110.

A darker pattern (pl. 12, fig. 19) has the first half of last whorl light brownish vinaceous, banded and shaded with russet vinaceous, last half whorl almost solid vinaceous brown faintly lined and streaked with a lighter tint.

A white specimen (pl. 12, fig. 19a) lacks color except for the cream-buff embryonic whorls and a line of ochraceous tawny on the outer margin or back edge of the lip. Plate 12, figure 19b, shows a rare pink color form with the postembryonic whorls a very dilute tint of pale flesh color deepening to flesh color on the last whorl, 3.5 mm. behind the edge of the lip the color deepening to vinaceous pink.

**ACHATINELLA APEXFULVA VESPERTINA** Baldwin

PLATE 3, FIGURE 28; PLATE 12, FIGURES 23-25

*Achatinella vespertina* BALDWIN, Proc. Acad. Nat. Sci., Philadelphia, 1895, p. 219, pl. 10, fig. 14.—PILSBRY and COOKE, Man. Conch., vol. 22, p. 322, pl. 60, figs. 2, 3, 1914.

The holotype in the Academy of Natural Sciences (pl. 12, fig. 23) has the embryonic whorls cartridge buff shading to light pinkish cinnamon on the last half embryonic whorl; postembryonic whorls light pinkish cinnamon; impressed sutural band cartridge buff; lip and columella callus cartridge buff. Length 20.6 mm., greater diameter 14.3 mm., number of whorls 6 $\frac{3}{4}$ .

Distribution, area 98?: **Kawailoa**, D. D. Baldwin, type lot, BBM 57996, 5 dextral, also BBM 54685, 54737, 6 dextral, E. Lyman ex Baldwin, BBM 167354, 9 dextral; **Kamoku**, J. S. Emerson, BBM 102310-102311; **Waialua**, J. S. Emerson, BBM 102309; "Kawaiiki  $\frac{1}{2}$  way down the valley, side north of 2nd Kamoku Plateau." (O. P. Emerson label in O. H. Emerson collection, BBM 103983.) "In a secondary ravine of Kawaiiki Valley on the South side, not quite as far up the valley as the hut back of Kamoku." (O. P. Emerson label in MCZ.) Also collected by Wilder, BBM 50605, and Spalding in **Kawaiiki Gulch**. The Wilder lot has no label but is localized from the Spalding collection. Spalding collected with Wilder, and on his authority the approximate area 98? is marked on fig. 5a, page 105.

The usual form and color pattern of the shell (pl. 3, fig. 28) has been selected from the Baldwin and Lyman lots. The embryonic whorls are light buff; postembryonic whorls pale ochraceous salmon with a faint band on the last two whorls just above the edge of the periphery of pale cinnamon pink, on the last whorl, below this band, is a line of the same color; impressed sutural band the ground color; lip and columella callus pale ochraceous salmon. Length 19.6 mm., greater diameter 13.1 mm., spire height 10.8 mm.

In a lot in the Wilder collection the usual form (pl. 12, fig. 24) has a more obese appearance, and also shows a pinkish-hued form which does not occur in the type lots; embryonic whorls pale pinkish buff; first postembryonic whorl and a half pale pinkish buff faintly streaked with pinkish buff, last postembryonic whorl and a half vinaceous pink spirally banded and lined with pale vinaceous fawn; impressed sutural band pale pinkish cinnamon; lip and columella callus white or a dilute tint of lilac buff. Length 19.1 mm., greater diameter 13.4 mm., spire height 10.5 mm.



A narrow shell (pl. 12, fig. 25) measures: Length 19.5 mm., greater diameter 11.6 mm., spire height 11.5 mm.; embryonic whorls white; first two postembryonic whorls a dilute tint of tilleul buff, last whorl a very dilute tint of seashell pink spirally banded and lined above and below the wide peripheral band with seashell pink.

**ACHATINELLA APEXFULVA KAHUKUENSIS** Pilsbry and Cooke

PLATE 3, FIGURE 34; PLATE 11, FIGURES 32-33a

*Achatinella valida kahukuensis* PILSBRY and COOKE, Man. Conch., vol. 22, p. 338, pl. 52, figs. 17-17a, 1914.

To quote from Pilsbry and Cooke:

The shell is dextral, white above, yellow below the periphery, usually encircled with a black-brown line at the junction of the two ground-tints, and often there are several additional lines widely spaced on the base or sometimes above. A faint sutural line may usually be discerned. Embryonic whorls when unworn are cartridge buff, slightly darker near the sutures, but not at the tip. The outlines of the spire are perceptibly concave, the last whorl swollen. Lip moderately thickened, white; columella very faintly rose-purple.

Length 20, diam. 13 mm.;  $6\frac{1}{2}$  whorls.

Length 18.7, diam. 12.2 mm.;  $6\frac{1}{2}$  whorls.

Oahu: Kahuku, at an elevation of 1,500 to 1,750 ft. (L. A. Thurston). Co-types in collection A. N. S. and Bishop Mus., from Mr. Thurston's Collection.

Distribution, area 115?: **Malaekahana-Laie Ridge**, Thurston BBM 130973. From Thurston's description of the locality, the ridge is undoubtedly the **Malaekahana-Kaluakauila Ridge**. The exact location is not known but tentatively may be placed in area 115?. (fig. 6a, p. 185). Also collected by Wilder, BBM 50608, J. S. Emerson, BBM 102339.

The shell of Pilsbry's plate 52, figure 17, is here reproduced on plate 11, figure 32, and is considered the lectotype because it has the usual color pattern of the shell. The color pattern of the lectotype is similar to that of plate 3, figure 34, which is an obese form of the shell, and has the first two and a half embryonic whorls worn and cream color, last embryonic whorl white; postembryonic whorls above the periphery white, last whorl, below the peripheral band of burnt umber, honey yellow with two central lines of cinnamon; outer margin of the lip avellaneous, inner margin white, columella callus light vinaceous fawn. Length 19.4 mm., greater diameter 13.5 mm., spire height 10.5 mm.

A lighter color pattern (pl. 11, fig. 33) has the embryonic whorls light buff; postembryonic whorls white, shaded or faintly banded with pale mouse gray, on the penultimate whorl a band of cinnamon on the upper third of the whorl fading out on the last whorl, last

whorl banded at the periphery with a band of amber brown, below the periphery the first half of the last whorl chamois shading to white on the last half of the whorl, entire whorl lined with natal brown, the last half of the whorl more profusely lined and banded than the first half; impressed sutural band wood brown; lip and columella callus light vinaceous buff.

One shell in the Thurston lot (pl. 11, fig. 33a) has the post-embryonic whorls white, banded just above or at the edge of the periphery with natal brown, on the last whorl the band or line fades to army brown and on the last half of the whorl to a line of cinnamon, within and just outside the aperture the shell callus honey yellow; impressed sutural band white. Length 20.3 mm., greater diameter 13.3 mm., spire height 10.8 mm.

A narrow shell measures: Length 18.0 mm., greater diameter 11.5 mm., spire height 10.3 mm.

#### GROUP OF A. A. APEXFULVA DIXON

#### ACHATINELLA APEXFULVA APEXFULVA Dixon

#### PLATE 3, FIGURE 27; PLATE 11, FIGURES 17-19

*Helix Apex Fulva* DIXON, A voyage round the world; but more particularly to the north-west coast of America, p. 354, *Turbo Apex Fulva* Dixon, on unnumbered plate, 1789.

*Achatinella apexfulva* DIXON, Pilsbry and Cooke, Man. Conch., vol. 22, 317, pl. 50, fig. 15; pl. 60, figs. 1-1b (only), 1914.

*Turbo lugubris*, etc., CHEMNITZ, Neues Syst. Conch. Cabinet, vol. 11, p. 278, pl. 209, figs. 2059-2060, 1795.

*Helix lugubris* CHEMNITZ, Férussac, Tabl. Syst., Fam. Limaçons, p. 56, 1821 (not *Helix lugubris* Gmelin, Syst. Nat., vol. 13, p. 3665, 1791).—FÉRUSAC, in Freycinet's Voyage autour du Monde de l'Uranie et la Physicienne, Zoologie, p. 479, 1824.—VON MARTENS, Malakozool. Blätt., vol. 19, p. 40, 1872.

*Achatinella lugubris* CHEMNITZ, Pfeiffer, Monographia Heliceorum Viventurum, vol. 2, p. 239, 1848; vol. 3, p. 465, 1853; vol. 4 p. 542, 1859; vol. 6, p. 177, 1868.—REEVE, Conch. Icon., vol. 6, Achatinella, pl. 2, fig. 10a (not 10b), April 1850.

*Monodonta seminigra* LAMARK, Hist. Nat. Anim. sans Vert., vol. 7, p. 37, 1822; 2d ed., Deshayes and Edwards, vol. 9, p. 181, 1845.—DELESSERT, Recueil de Coq., Decrites par Lamark, pl. 37, figs. 2a-c, 1841.

*Bulinus seminigra* MENKE, Synops. Method. Moll., 2d ed., p. 26, 1830.

*Achatinella pica* SWAINSON, Quart. Journ. Sci., Lit., and Art, January-March, p. 84, 1828; Zool. Illustr., ser. 2, vol. 3, p. 99, pl. 99, fig. 1, 1832-1833.

To quote from Dixon:

. . . . the natives form necklaces, bracelets, and other ornaments: one of these necklaces afforded a singular species of the *Helix* genus of Linnaeus, which I was informed is a fresh-water shell. It is outwardly smooth, has seven spires,

and is of a black-brown colour, except the tip, which is pale-yellow: the inside is smooth and white, and the mouth is margined within. It is remarkable for a knob or tooth on the columella, but which does not wind round it, consequently excludes it from the *Voluta* genus of Linnaeus, to which at first sight it appears to be related. As I presume it to be a species hitherto undescribed, I have taken the liberty to give it the trivial name of *Apex Fulva*, or the *Yellow Tip*. A figure of it, in two views, is given in one of the following plates.

Specimens of this kind are in the Leverian Museum.

Distribution, area 97: "Picked before 1861 in Opaëula Valley on the south side opposite ridge running down over the tunnel. Picked on ieie [*Freycinetia*], kawau [keawau=*Ilex*], kopiko [*Straussia*], kolea [koolea=*Myrsine*]." (O. P. Emerson label for his lot of *A. a. apexfulva* in MCZ.) "Opaëula Gulch, Waialua," J. S. Emerson, BBM 102270, 102272; Kamoku, J. S. Emerson, BBM 33298; Opaëula Gulch, locality 330-4, elevation 1,100 feet, Welch, K. Emory, and W. Giffard, 15 dead dextral 1935. This locality is on the south side of the Gulch and answers O. P. Emerson's description of his locality, and is probably the place where the Emerson brothers got their material (see figs. 5, 5a, p. 105).

According to Murray (1904, p. 175) the Leverian Museum was formed by Sir Ashton Lever (1729-1788) in the early years of his life at his house, Alkington Hall, near Manchester. In 1783 the museum was sold by lottery. The lottery was won by James Parkinson. In 1806 the museum was sold at auction. In a copy of the sales catalog of the Leverian Museum, in my possession, there are 10 lots which mention necklaces, bracelets, and other ornaments, made of shells, from the Sandwich Islands. One of these ornaments may be the one Dixon refers to, which contains the type or paratypes of *A. a. apexfulva*. The lei (necklace) Dixon studied may have been broken up and the specimens sold. Dixon's original figure is reproduced on plate 11, figure 17.

Pilsbry and Cooke (1914, p. 321) give such a good account of the history of *A. a. apexfulva* that it seems unnecessary to review the matter again. In discussing the origin of shell leis Pilsbry says:

It appears that shell leis were strung by the natives of the good agricultural region about Waialua Bay, who doubtless got the shells from the lower forests in the back country, in various places in Kawaihoa and Helemano districts. They were carried or traded eastward, and so obtained by explorers harboring at Honolulu. It is altogether likely that all of the *A. apexfulva* of these leis were from some one colony in Opaëula Gulch.

Pilsbry correctly considers *Turbo lugubris*, *Monodonta seminigera*, and *A. pica* synonyms of *A. a. apexfulva*. The types of these forms

are not available to me and may be lost. It is possible that *lugubris* and *seminigera* come from the same lei Dixon used. If the shells came from another lei there is a possibility that the shells are different from *apexfulva*. But until the types are seen it is impossible to say what the shells really are, and Pilsbry's identification should stand. Swainson's shells were collected by Captain Byron of H. M. S. *Blond*. These again could have come from elsewhere than the type locality of *apexfulva*. Again until the type is studied it is difficult to say whether the shell is or is not *A. apexfulva*. The Swainson shells may be forms from area 94 of *A. a. beata* var. 1, which are impossible to separate from typical *A. a. apexfulva*. Therefore, even were the types available for all three forms they might be from different localities and yet not separable from *A. a. apexfulva*, so that it is best to consider them synonyms.

Since the holotype of *A. a. apexfulva* has not been located, the shells in the J. S. Emerson lot in the Bishop Museum, the Academy of Natural Sciences, and the O. P. Emerson lot in the Museum of Comparative Zoology will be considered typical. The usual form and color pattern in the J. S. Emerson lot (pl. 3, fig. 27) has the embryonic whorls light buff; postembryonic whorls hessian brown or maroon; impressed sutural band the color of the ground with the upper extreme edge pale pinkish buff; lip and columella callus pale vinaceous fawn. Length 18.8 mm., greater diameter 12.3 mm., spire height 10.8 mm., number of whorls  $6\frac{1}{2}$ .

An extreme obese form (pl. 11, fig. 18) measures: Length 18.8 mm., greater diameter 13.3 mm., spire height 10.2 mm.; the color pattern is similar to figure 27 except that the last whorl is faintly streaked with tawny. Eight specimens in the Emerson lot of 38 specimens have a gray streaked pattern similar to plate 11, figure 18a; last two postembryonic whorls maroon, streaked with pale quaker drab, the streaks cut by lines of maroon. Length 19.1 mm., greater diameter 12.3 mm., spire height 11.0. Pilsbry's plate 60, figure 1c, does not look like *A. a. apexfulva*, but rather like the lined form, or *A. a. aloha* var. 1. No such color pattern is found in the J. S. Emerson lots from Opaepala. The shell may be a rare color pattern of an intermediate race which occurred between *A. a. apexfulva* and *A. a. duplocincta*. Then again it may be a stray shell that was mixed in with the shells of *A. a. apexfulva*.

An adult shell from locality 330-4 is shown on plate 11, figure 19.

## ACHATINELLA APEXFULVA DUPLOCINCTA Pilsbry and Cooke

PLATE 3, FIGURE 26; PLATE 12, FIGURES 27, 28

*Achatinella apexfulva* color form *duplocincta* PILSBRY and COOKE, Man. Conch., vol. 22, p. 323, pl. 55, figs. 6-8, 1914.

To quote from Pilsbry and Cooke:

The shell is dextral, white, encircled with two chestnut bands or group of lines, one at the periphery, the other below it; lip faintly violaceous. Length 18, diam. 11 mm. Length 17, diam. 11.7 mm.

The cotypes of this form are 1272, 1273 Cooke coll., 108776 A. N. S., and 1213 Gulick coll., Boston Soc. The former lots are labelled "Wahiawa, Emerson, extinct?", three banded specimens, one drawn in fig. 8, and two in which the bands are very faint, a little stronger near the lip. The locality seems open to doubt. The Gulick lot is from "Kawailoa, east side."

Distribution, area 97A??: Type locality **Kawailoa, Waialua**, "on a group of 3 or 4 trees at the head of a little gulch beside and to the north of the road to Kamoku, some two miles makai [toward the sea] of Kamoku, collected by J. S. Emerson previous to the year 1863." (J. S. Emerson label, BBM 102312.) The original label on the O. P. Emerson shells in the Museum of Comparative Zoology reads: "Picked before 1861 in a secondary ravine branching S. from the Kamoku reservoir valley below the narrows which is now a grassy hollow. An old Akakea tree [*Bobea* sp.?] bore the shells—all now extinct—and not found elsewhere by me." The shell of Pilsbry and Cooke's plate 55, figure 8, here reproduced on plate 12, figure 27, is selected for the lectotype. The label Wahiawa on the Cooke type lot is surely erroneous, because the shells came from J. S. Emerson who obtained his specimens from Kawailoa. From the above data of the Emerson brothers, *A. a. duplocincta* was a lowland race that occurred below the colony of *A. a. apexfulva*, which probably occurred in Opauala Gulch area 97 and was somewhere along the road on the top of the Opauala-Kawailoa Ridge. Area 97A?? is the probable region of the type locality (fig. 7, p. 194).

The usual form and color pattern in the type lot in the J. S. Emerson collection (pl. 3, fig. 26) is a white shell, with a single line of cinnamon above the periphery on the last whorl, and four lines of mikado brown below the periphery; lip and columella callus light pinkish cinnamon. Length 17.9 mm., greater diameter 11.8 mm., spire height 10.0 mm., number of whorls 6½.

A narrow specimen and darkest color form (pl. 12, fig. 28) is a white shell banded just above the periphery on the last two whorls with two bands of mikado brown, above which on the last whorl and



a half are three faint lines of cinnamon, base banded with four bands of burnt umber. Length 17.3 mm., greater diameter 10.7 mm., spire height 9.6 mm. An obese shell measures: Length 17.1 mm., greater diameter 12.6 mm., spire height 9.2 mm.

**ACHATINELLA APEXFULVA BAKERI, new subspecies**

PLATE 3, FIGURE 30; PLATE 11, FIGURES 20-20b

The shell is small, the last whorl is usually yellow, and has a characteristic yellow subperipheral band. The form is extinct today. It probably came from an isolated lowland locality. No intermediates have been located by me connecting it to any other race of *A. apexfulva*. The strongly axially streaked color pattern is similar to *A. a. apicata* or *A. a. wahiawa*. The presence of the subperipheral band may cause this form to be confused with *A. a. gulickii*. But *A. a. bakeri* mainly differs from both forms in the yellow color pattern of the last whorl.

The embryonic whorls of the holotype (pl. 3, fig. 30) are light ochraceous buff; first half postembryonic whorl vinaceous fawn axially streaked with white, next half whorl pale drab gray axially streaked with light brownish drab, last whorl and a half naples yellow axially streaked with straight and zigzag streaks, speckled and lined with mars brown, below the edge of the periphery a band of naples yellow; impressed sutural band pale pinkish buff; lip and columella callus tilleul buff. Length 16.4 mm., greater diameter 11.5 mm., spire height 8.5 mm. The usual form was not determined because of the paucity of specimens.

Distribution, area?: **Waimea**, J. S. Emerson, BBM 102333, A. F. Judd ex J. S. Emerson, BBM 162334. "Found on a Plateau north of Waihalona [Kawaihalona?] Gulch below North Branch on pua [*Osmanthus*] tree on a clump in open plain." (O. P. Emerson collection, MCZ.) This form is named after Dr. H. B. Baker, of the University of Pennsylvania.

The shell may be narrower (pl. 11, fig. 20) and have a vivid yellow ground; the first postembryonic whorl brownish drab axially streaked with white or pale drab gray, last two whorls yellow ocher axially streaked with natal brown, just below the edge of the periphery a band of yellow ocher. Length 18.2 mm., greater diameter 11.5 mm., spire height 10.5 mm.

A lighter color pattern and an obese shell (pl. 11, fig. 20a) has the first half postembryonic whorl axially streaked with light cinnamon drab and white, penultimate whorl pale pinkish cinnamon or white,

streaked with light brownish drab, last whorl cream buff lightly streaked with straight and zigzag streaks of verona brown, about the periphery and base, bands of cream buff. Length 17.5 mm., greater diameter 11.8 mm., spire height 8.7 mm.

The last whorl may not have a wide yellow peripheral band (pl. 11, fig. 20b); first postembryonic whorl axially streaked with brownish drab or deep brownish drab and pallid mouse gray, penultimate whorl streaked with deep quaker drab and pallid mouse gray, last whorl pale pinkish buff shaded with cream buff axially streaked with sepia and warm sepia. Length 17.3 mm., greater diameter 11.0 mm., spire height 9.3 mm.

### ACHATINELLA APEXFULVA LEUCOZONA Gulick

PLATE 3, FIGURE 31; PLATE 11, FIGURES 28-31

*Apex leucozonus* GULICK, Proc. Zool. Soc. London, 1873, p. 83, pl. 10, fig. 6.  
*Achatinella valida cinerosa* PFEIFFER, Pilsbry and Cooke, Man. Conch., vol. 22, pp. 337, 338, pl. 55, figs. 9-16, 1914.

The embryonic whorls of the holotype (pl. 11, fig. 29) are cartridge buff, last half embryonic whorl banded on the lower fourth of the whorl with a band of a light tint of isabella color; postembryonic whorls pale drab gray, first two postembryonic whorls axially streaked with benzo brown and lined with drab, last whorl banded and axially streaked with snuff brown darkening to verona brown on the last half whorl. Length 18.2 mm., greater diameter 12.7 mm.

Distribution, area?: Type locality **Waialei** [**Waialea**], Gulick, BBM, ANSP 92656; **Waialea**, J. S. Emerson, BBM 102337. Holotype, MCZ 39906.

*A. a. leucozona* is either a highland or a lowland form of *A. a. napus*. The shell of plate 11, figure 28, looks like an intermediate form between *A. a. napus* and *A. a. leucozona* but closest to the color pattern of *A. a. leucozona*. The embryonic whorls are light buff; first postembryonic whorl light buff, streaked with mikado brown, penultimate whorl a yellowish tint of avellaneous streaked with wood brown, and lined and banded with pinkish buff, last whorl above the periphery banded and lined with pinkish buff and a narrow and a wide band of buckthorn brown, at the edge of the periphery a band of light buff, and a subperipheral band of raw sienna, base raw sienna banded with a wide band of a light tint of antique brown axially streaked with antique brown, below which is a line of argus brown.

The usual form of the shell (pl. 3, fig. 31) in the Gulick ANSP lot has the embryonic whorls white; first two postembryonic whorls

light drab faintly spirally lined with white and strongly axially streaked with cinnamon drab, last whorl wood brown axially streaked with straight and zigzag streaks of wood brown, fawn color, and light pinkish buff, and faintly spirally lined with white and wood brown, just below the edge of the periphery a line of white; impressed sutural and subsutural bands white; lip pale ochraceous buff, columella callus white. Length 17.7 mm., greater diameter 11.4 mm., spire height 9.9 mm.

The lightest color pattern and obese form of the shell (pl. 11, fig. 30) has the first postembryonic whorl pale drab gray, banded and streaked with light cinnamon drab, penultimate whorl pale ecru drab banded and streaked with ecru drab, first half of the last whorl a light tint of pale ecru drab, lined and streaked with ecru drab, last half whorl pale vinaceous fawn, lined and faintly streaked with light vinaceous fawn; impressed sutural and subsutural bands white. Length 17.7 mm., greater diameter 12.0 mm., spire height 9.3 mm.

A darker color pattern than the usual one and a narrower form of the shell (pl. 11, fig. 30a) has the postembryonic whorls snuff brown axially streaked with russet and mars brown, and lined with a line of mars brown on the upper third of the whorl, about the periphery a band of white, lined or banded with mars yellow; impressed sutural band light ochraceous buff lightening to light buff on the last whorl. Length 17.7 mm., greater diameter 10.8 mm., spire height 9.6 mm.

The embryonic whorls of the darkest color pattern (pl. 11, fig. 31) are light buff shading to ochraceous salmon; postembryonic whorls warm sepia lightened by occasional axial streaks of mikado brown, last whorl banded just below the edge of the periphery with a band of pale cinnamon pink lined and streaked with mars yellow, on the first half of the last whorl a basal band of ochraceous orange; impressed sutural band pale pinkish buff darkening to light ochraceous buff on the last half whorl; lip and columella callus pale pinkish cinnamon deepening to pale vinaceous fawn on the outer margin. The color pattern is a rare one in the Gulick ANSP lot, but the usual one in the J. S. Emerson lot.

#### ACHATINELLA APEXFULVA NAPUS Pfeiffer

##### PLATE II, FIGURES 25-27

*Achatinella napus* PFEIFFER, Proc. Zool. Soc. London, 1855, p. 5, pl. 30, fig. 19.  
*Achatinella mustelina sordida* NEWCOMB, Pilsbry and Cooke, Man. Conch., vol. 22, p. 349, pl. 30, fig. 19 (only), 1914.

The holotype (pl. 11, fig. 25) in the British Museum is marked with a red spot of sealing wax. The embryonic whorls are white;

first two postembryonic whorls cartridge buff, last whorl above the periphery vinaceous buff, at the edge of the periphery a band of cartridge buff or white, below the periphery banded with vinaceous buff, basal band about the umbilicus cartridge buff or white with faint lines of vinaceous buff; lip cartridge buff banded with vinaceous buff. Length 19.4 mm., greater diameter 10.8 mm., spire height 12.0 mm., number of whorls  $6\frac{5}{8}$ .

Distribution, area?: **Waialei [Waialeale]**, Gulick.

The shell may have a yellow base (pl. II, fig. 26) embryonic whorls white; postembryonic whorls pale cinnamon pink; suture and sub-sutural bands slightly more dilute tint of cinnamon pink; peripheral band white, below the periphery chamois; lip and columella callus tilleul buff. Length 19.9 mm., greater diameter 12.0 mm., spire height 11.6 mm.

A larger specimen (pl. II, fig. 27) shows a darker pink color pattern and a more inflated last whorl. The postembryonic whorls are pale vinaceous fawn, banded on the lower half of the whorl above the periphery with a band of light vinaceous buff which darkens to vinaceous buff streaked with light vinaceous buff on the penultimate, and on the last whorl buff pink streaked with vinaceous buff, at the edge of the periphery a band of white, base yellow ocher lined with buckthorn brown; lip vinaceous buff, columella white. Length 20.0 mm., greater diameter 12.5 mm., spire height 11.5 mm.

**ACHATINELLA APEXFULVA PAUMALUENSIS**, new subspecies

PLATE 3, FIGURE 32; PLATE II, FIGURES 21, 21a

The subspecies is a highland gray race closely related to *A. a. napus*. The embryonic whorls of the holotype (pl. 3, fig. 32) are pale pinkish buff with a line of pinkish buff in the center of the lower third of the whorl; first postembryonic whorl upper half white or pallid mouse gray, lower half sorghum brown shading to pale mouse gray axially streaked with zigzag lines of benzo brown, remaining whorls spirally banded with fuscous or fuscous black, ground pale mouse gray up to the last half whorl which is shaded with light vinaceous fawn, below the periphery last whorl isabella color banded with fuscous; upper third of the impressed sutural band white or tilleul buff, remainder of the band shading from vinaceous buff to vinaceous fawn and fawn color on the last half whorl. Length 18.3 mm., greater diameter 12.2 mm., spire height 10.0 mm., number of whorls  $6\frac{1}{8}$ .

Distribution, area III: **Paumalu-Kaunala Ridge**, type locality 431 elevation 1,000-1,050 feet, Meinecke, 1933 (fig. 6, p. 185). Also collected by Thurston, BBM 130915.

The shell may be more strongly banded (pl. 11, fig. 21) and more obese; postembryonic whorls pallid mouse gray faintly axially streaked with mouse gray, above the periphery spirally ornamented with faint lines and a band of warm blackish brown, base naples yellow banded with warm blackish brown; the impressed sutural band vinaceous fawn on the first whorl, on the penultimate the ground color, on the last whorl the base of the band shaded with warm blackish brown. Length 18.8 mm., greater diameter 13.0 mm., spire height 9.5 mm.

One specimen (pl. 11, fig. 21a) has the postembryonic whorls warm blackish brown, banded on the first whorl with white, the remaining whorls with extremely faint lines of white or pallid mouse gray. Length 18.0 mm., greater diameter 12.1 mm., spire height 8.8 mm.

**ACHATINELLA APEXFULVA OIOENSIS, new subspecies**

PLATE 3, FIGURE 33; PLATE 11, FIGURES 22, 22a

The shell is a close relative of *A. a. paumaluensis*, but having a series of different color patterns; the embryonic whorls of the holotype (pl. 3, fig. 33) are pale pinkish cinnamon; postembryonic whorls above the periphery diamine brown, below the edge of the periphery of the last whorl ochraceous buff finely axially streaked with ochraceous tawny, spirally banded with a band of diamine brown and fine lines of russet, in the umbilical region a patch of black or diamine brown; impressed sutural band diamine brown; lip and columella callus fawn color. Length 18.0 mm., greater diameter 11.5 mm., spire height 10.3 mm.

Distribution, area 114: Oio-Oio East Branch Ridge, type locality 460A, elevation 1,300 feet, Meinecke, 1933 (figs. 6, 6a, p. 185).

The color pattern may lack the yellow base (pl. 11, fig. 22); postembryonic whorls liver brown, last whorl and a half faintly banded above the periphery, last whorl just below the edge of the periphery with a band of mars yellow almost obscured by axial streaks of liver brown; lip and columella callus pale vinaceous fawn, outer edge of the lip bone brown; impressed sutural band the color of the ground. The lightest color pattern (pl. 11, fig. 22a) has the postembryonic whorls light buff deepening to ochraceous buff on the last whorl, axially streaked with tawny, last whorl and a quarter at the edge of the periphery and about the base banded with diamine brown; impressed sutural band black. Length 17.0 mm., greater diameter 12.3 mm., spire height 8.7 mm.



## ACHATINELLA APEXFULVA OIOENSIS var. 1

## PLATE II, FIGURES 23-23b

Distribution, area 112: Pahipahialua Gulch, locality 450, elevation 1,250 feet, Meinecke, 1933 (figs. 6, 6a, below); also collected by Wilder, BBM 50612.

The color patterns of area 112 at first glance seem the same as those of typical *oioensis* (area 114), but close examination shows that

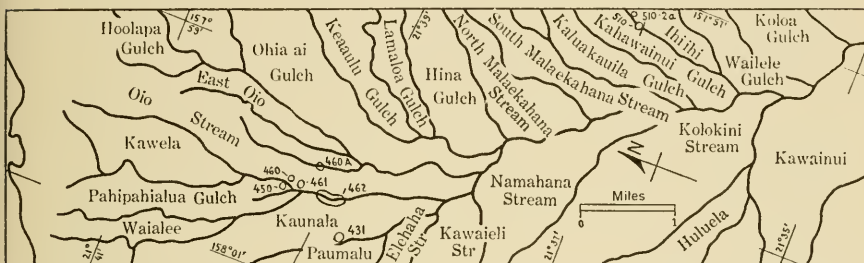


FIG. 6.—Northern Oahu, windward slope of the Koolau Range, the northwestern half of region IV (fig. 7, p. 194), showing localities of subspecies of *A. apexfulva* belonging to the groups of *A. a. apexfulva* and *A. a. aloha*.

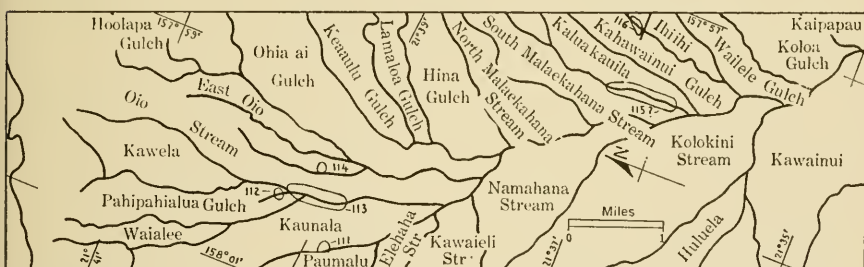


FIG. 6a.—Same as fig. 6, but showing the areas of distribution of the subspecies of *A. apexfulva* belonging to the groups of *A. a. apexfulva* and *A. a. aloha*.

slight variations occur. Usually the yellow ground color is lighter in area 112. A close reproduction of the patterns of plate 3, figure 33, and plate 11, figure 22a, is not found in area 114. Plate 11, figure 23, resembles figure 22a, but the characteristic wider sutural band of the yellow patterns of area 112 separates it from the Oio Stream forms of area 114. Moreover, dull brown forms with faint zigzag streaks occur in area 112 and do not occur in area 114.

The usual color pattern and the obese form of the shell (pl. 11, fig. 23) has the embryonic whorls pale pinkish buff; postembryonic whorls light buff very finely lined and streaked with ochraceous

tawny, at the edge of the periphery a thin band of dresden brown, base seal brown or black; sutural and subsutural bands verona brown darkening to seal brown or black on the last two whorls; lip fawn color, columella callus pale vinaceous fawn. Length 17.3 mm., greater diameter 12.6 mm., spire height 8.9 mm.

A zigzag pattern and elongate form of the shell is shown on plate 11, figure 23*a*; last two postembryonic whorls are verona brown faintly axially streaked with zigzag and straight streaks of tawny olive; impressed sutural band the ground color. Length 19.0 mm., greater diameter 12.3 mm., spire height 10.4 mm.

Only four live specimens are known from locality 450. A dark color pattern (pl. 11, fig. 23*b*) seems to be an intermediate color form between figures 22 and 23*a* of plate 11. It may be fairly close to the usual form; the last two postembryonic whorls are seal brown, at the edge of the periphery a line of yellow ocher, below the periphery a band of ochraceous buff axially streaked or spotted with seal brown, the seal brown or black base is also streaked with patches or streaks of ochraceous buff. Length 18.0 mm., greater diameter 12.5 mm., spire height 9.2 mm.

#### **ACHATINELLA APEXFULVA OIOENSIS var. 2**

##### PLATE 11, FIGURES 24-24*d*

Area 113: **Pahipahialua-Oio Ridge**, locality 460, elevation 1,150-1,200 feet, 3 dextral; 461, elevation 1,250-1,300 feet, Meinecke, 33 dextral 1933; **Kaunala-Oio Ridge**, locality 462\*, elevation 1,300-1,376 feet, Meinecke, 1914 (figs. 6, 6*a*, p. 185). This form also collected by J. S. Emerson, BBM 102335-102336, O. H. Emerson, BBM 103986, Thurston, BBM 130954, 130950.

The shells resemble those of area 112 but have a different range of color patterns. The usual form and color pattern of the shell (pl. 11, fig. 24) has the embryonic whorls pale pinkish buff; first postembryonic whorl haematite red axially streaked with straight and zigzag streaks of pale olive gray, the last whorl and a quarter above the periphery lighter in color, being more streaked with pale olive gray and banded at the edge of the periphery with a band of pale olive gray tinted on the first half of the whorl with chamois, the base warm sepia lined with chamois; impressed sutural band mikado brown; lip and columella callus pale vinaceous fawn. Length 19.7 mm., greater diameter 12.8 mm., spire height 10.6 mm.

The color pattern may be lighter and the base yellow (pl. 11, fig. 24*a*); first postembryonic whorl and three-quarters cinnamon

drab faintly axially streaked with drab gray, below the impressed sutural band of fawn color two lines of tilleul buff, on the last whorl the ground above the periphery tilleul buff faintly axially streaked with straight and zigzag streaks of avellaneous, base mustard yellow with a band of avellaneous just below the subperipheral mustard yellow band, umbilical region lined with tawny.

An elongate shell (pl. 11, fig. 24*b*) and a variant of figure 24*a* has the postembryonic whorls white, tinted, faintly lined, and faintly axially streaked with tilleul buff or vinaceous buff; sutural and wide subsutural bands and the line below the subsutural band wood brown; on the last whorl a thin band at the edge of the periphery of drab, below which the ground is chamois banded with wood brown. Length 18.2, greater diameter 11.8 mm., spire height 10.3 mm.

The lightest color pattern (pl. 11, fig. 24*c*) has the white postembryonic whorls above the periphery lined with a faint line of naples yellow on the last whorl, below the periphery naples yellow with a central line of cinnamon, and a line and a band of russet in the umbilical region; sutural and wide subsutural bands chocolate.

A yellow color pattern (pl. 11, fig. 24*d*) has the first two postembryonic whorls pale pinkish buff, last whorl light buff finely spirally lined and axially streaked with ochraceous tawny, on the base a thin band of russet and faint lines of tawny; impressed sutural band and thin subsutural band mars brown. The wide subsutural banded form of figure 23 also occurs in this area.

**ACHATINELLA APEXFULVA IHIIHIENSIS**, new subspecies

PLATE 3, FIGURE 35; PLATE 11, FIGURE 34

The form is closely related to *A. a. kahukuensis* but differs in color pattern. The color pattern of the holotype resembles that of *A. a. oioensis*, but *ihiihiensis* has a base colored a lighter shade of yellow. The embryonic whorls of the holotype (pl. 3, fig. 35) are cream color; postembryonic whorls warm blackish brown; impressed sutural band cinnamon; edge of the periphery and all below the periphery of the last whorl mustard yellow, banded with a central band of warm blackish brown and two lines of mikado brown; lip and columella callus light vinaceous fawn, lip streaked with white. Length 17.7 mm., greater diameter 11.6 mm., spire height 9.6 mm., number of whorls 6.

Distribution, area 116: **Ihiihi-Kahawainui Ridge**, type locality 510, elevation 1,250-1,300 feet, Meinecke, 12 dextral 1932-1934; also locality 510-2a, elevation 1,150-1,200 feet, Welch, 10 dead specimens, 1935 (figs. 6, 6*a*, p. 185).

The shell may have a lighter color pattern (pl. 11, fig. 34); embryonic whorls light buff, faintly lined on the last half whorl with ochraceous tawny; first postembryonic whorl white, shaded with pale gull gray and banded with a central band of mars brown in the center of which is a black line, a lower band just above the periphery bone brown, divides into two lines on the last half of the penultimate, the ground on the last half of the penultimate is faintly shaded with mustard yellow, last whorl mustard yellow, banded above, below, and at the periphery with a band of bone brown at the lower edge of which is a band of mikado brown, just above the edge of the periphery are two lines, an upper of mikado brown, and a lower of bone brown, both of which fade to a lighter tint on the last half whorl; the impressed sutural band darkens from mikado brown on the first whorl to warm sepia on the last whorl. Length 18.5 mm., greater diameter 12.6 mm., spire height 9.5 mm.

**ACHATINELLA APEXFULVA WAILELENSIS, new subspecies**

PLATE 3, FIGURE 36; PLATE 11, FIGURE 35

The shell is not closely related to any of the known forms of *A. apexfulva*. The locality occurs far away from all the known localities of *A. apexfulva* and no intermediates between *wailelensis* and any other form are known. The shell, however, has the usual form of *A. apexfulva* and resembles *A. a. roseata* of Waimano Stream. The holotype (pl. 3, fig. 36) has the embryonic whorls white; first postembryonic whorl fawn color, last two whorls vinaceous fawn; impressed sutural band pinkish buff; lip pinkish buff, columella callus white. Length 17.3 mm., greater diameter 12.0 mm., spire height 10.3 mm., number of whorls 6.

Distribution, area, 117: **Wailele Gulch**, locality 529-1, elevation 20 feet, collected by Mr. and Mrs. G. W. Russ, and Welch 1933. The shells are found in a fossil state in a stone outcropping near the Kamehameha highway (fig. 7, p. 194).

An obese form of the shell (pl. 11, fig. 35) measures: Length 17.1 mm., greater diameter 11.9 mm., spire height 8.7 mm.; postembryonic whorls shell pink axially streaked with buff pink. A narrow specimen measures: Length 17.6 mm., greater diameter 11.2 mm., spire height 9.4 mm.

CONCLUSIONS

Gulick (1905), Pilsbry and Cooke (1912-1914) considering various species of *Achatinella* from Hawaii, and Crampton (1916, 1932) in

a study of the species of *Partula* on Tahiti and Moorea, have pointed out that tree snails vary from valley to valley in various characteristics such as size, color pattern, and form of the shell. Welch (1938) pointed out that *A. mustelina* from the Waianae Mountains of Oahu, Hawaii, not only varied from valley to valley in different characteristics, but also at different elevations on the same ridge or in the same valley.

Before discussing the variation of *Achatinella apexfulva* I will explain what is meant by a highland and lowland form. On a basis of a group of characteristics such as color pattern of the embryonic and postembryonic whorls, shape and size of the shell, I have divided the material into highland and lowland forms. On figure 7 (p. 194) two broken lines drawn across the Koolau Range outline the three zones of shell variation. Zone I contains extreme lowland forms and is probably the region where many of the extinct Gulick forms were collected. The zone occupies all the region below the lowest broken line, which extends from just above areas 117, 97A??, 37?, to just below areas 1 and 2.<sup>2</sup> Zone II contains the usual lowland forms. Gulick collected or obtained material from the lower part of this zone. Zone II occupies all the region between the two broken lines. Zone III is inhabited by highland forms and extends from above zone II to the backbone ridge of the Koolau Range. Along the border of zones II and III forms occur in certain areas which can be classed as either highland or lowland shells on a number of characteristics. The placing of these borderline areas into highland or lowland zones has been a matter of judgment and might be done differently by another worker. Areas 5??, 6??, 7??, 14??, 65??, 66??, 78?, found on figures 3, 4, and 5, have been omitted from figures 7 and 8 because I am uncertain concerning the exact location of these areas.

In the following account of shell variation in each area, the usual form<sup>3</sup> and color pattern of the shell, generally exhibited on plates 1, 2, and 3, is taken as a basis for discussion. In some cases it was not possible to obtain a shell having both the usual form and color pattern. In that case only one of the group of characteristics is shown on one of the first three plates, such as the usual form of the shell or the usual color pattern, and the other characteristic is shown on another plate. In one case (pl. 1, figs. 27, 28) rare color patterns of a race

<sup>2</sup> An area is made up of a single locality or a group of localities containing similar forms or the same subspecies.

<sup>3</sup> See Welch (1938) for an account of how the usual form of the shell is selected.



are shown, which distinguish the area containing them from another area of similar shells.

#### A. HORIZONTAL VARIATION

##### 1. COLOR PATTERN OR COLOR OF THE EMBRYONIC WHORLS

On the color of the embryonic whorls the subspecies of *A. apexfulva* are segregated into four regions. Regions I and III have shells with bicolored embryonic whorls, and regions II and IV have unicolored embryonic whorls (fig. 7, p. 194). These four regions are further subdivided into intermediate regions Ia (area 19), IIa (areas 48, 48A, and the localities of area 47 occurring on the Manana-Waiawa Ridge), IIIa (areas 41, 42, 43, 63, and 64), IIIb (areas 61? and 62?), which contain intermediate or border forms between those of the main regions. The embryonic whorls of these border forms have a color pattern similar to that found on the shells at a similar elevation on the next parallel ridge to the southeast. This is also true of areas 40, 49, and 50.

In region IIIa the embryonic whorls are white, cream buff, or tan, faintly lined or banded with a lighter or darker color. They are intermediate between the white unicolored embryonic whorls of the group of *A. a. turgida* (region II) and the yellow banded bicolored embryonic whorls of the group of *A. a. polymorpha* (region III).

Region IIIb and areas 40, 49, and 50 definitely have the same colored embryonic whorls as found on the adjacent parallel ridge to the southeast. Region Ia contains shells with embryonic whorls which are still bicolored similar to the group of *A. a. simulans* (region I) to the southeast but are approaching the unicolored condition of the shells in region II. Region IIa has shells with slightly bicolored embryonic whorls intermediate between region II and III, but closest to the unicolored embryonic whorls of region II.

##### 2. COLOR PATTERN OR COLOR OF THE POSTEMBRYONIC WHORLS

Many difficulties are encountered in distinguishing subspecies using color pattern for a criterion, because the same color pattern occurs again and again in colonies of shells in widely separated areas. For example, the dark typical *apexfulva* pattern from area 97 or one very similar to it, may be found in area 35 (*A. a. turgida*) (fig. 7, p. 194), area 94 (*A. a. beata* var. 1), area 111 (*A. a. paumahuensis*), area 114 (*A. a. oioensis*). Pink patterns such as *A. a. lilacea* var. 1 in area 83 and *A. a. lilacea* possibly in area 83b?? may also be found in area 81??

(*A. a. punicca*), area 37? (*A. a. roseata*), and area 117 (*A. a. wailaleensis*). Somewhere near area 40 Wilder found specimens of *A. a. perplexa* (pl. 6, fig. 19d) which have a pattern similar to that of *A. a. lilacea*. The various forms of *A. a. rubidipicta* can easily be taken for specimens of *A. a. rubidilinea*. White color patterns of *A. a. ovum* (area 22), *A. a. cookei* var. 1 (area 39), *A. a. beata* var. 2 (area 108), and *A. a. roseipicta* (area 102), are very similar, differing only by a band or in the color of the lip. However, the range of color patterns of any one area always differs from that of another. Therefore, in considering horizontal variation not only the usual color pattern of the shell must be considered, but also the color pattern of the colony as a whole.

As has been pointed out before, *A. apexfulva* exhibits valley-to-valley or ridge-to-ridge variation, and the color patterns of widely separated localities are usually more strikingly different than those found on shells from adjacent areas. However, as in *A. mustelina* (Welch, 1938), *A. apexfulva* also exhibits vertical as well as horizontal variation. Therefore, when studying horizontal valley-to-valley variation it is important that both localities or areas under consideration are from approximately the same elevation or in the same lowland or highland zone such as zones I, II, or III.

I do not like to use the word elevation because two localities on opposite ridges may be at an equal distance from the backbone ridge and yet because of a hill on one ridge and a depression on the other, one locality may be definitely higher than the other. Again, one locality may be in a valley, the other on a nearby ridge, the two showing a wide difference in elevation. The distance a locality is from the backbone ridge or in what zone a shell is found is of greater importance than differences of several hundred feet in altitude. Therefore, zones and not differences in elevation will be discussed.

I have already noted above that the color of the embryonic whorls varies in regions I, II, III, IV. The color pattern of the shell not only shows marked variation between each of the four regions, but also less variation within each region. For instance a series of areas in region II zone II will have rather similar color patterns. In like manner a group of areas in region III zone II will have another series of similar patterns but which are markedly different from those found in region II zone II. In most areas occurring at similar elevations or in the same zone on opposite ridges in a certain region the color pattern of the shells are similar. However, in the region of Waimano Stream the color patterns of such opposite areas—for example, areas 44 and 43—are not similar. Area 44 has patterns

similar to those of area 50 above area 43 (fig. 4, p. 53). Also, the shells of area 45 on the Waimano-Manana Ridge more closely resemble the shells of area 49 above area 50, although area 50 is opposite area 45. In like manner the color patterns found in any zone in region III will definitely differ from those found in region IV. The same holds true for regions I and II.

In between the regions of major differentiation intermediate or border areas occur, such as regions Ia, IIa, IIIa, IIIb, and areas 40, 49, 50. Region Ia contains forms which have a color pattern intermediate between regions I and II, zone II, but closer to the color pattern of the shells to the southeast, or region I. Region IIa and IIIb and areas 49 and 50 have shells the color pattern of which is very similar to that of the shells to the southeast and entirely different from those to the northwest in the same zone. Region IIIa and area 40, zone II, contain gray color patterns which are close to the color patterns of region III, zone II, and very different from those to the southeast.

As a general rule more horizontal variation occurs in zone II than in zone III. This can be explained by the fact that usually the lower reaches of a ridge fans out into several long ridges. Consequently, there are more ridges and valleys at low elevations or in a lowland zone, which increases the possible number of isolated colonies in zones I and II as compared with zone III.

Today the isolation of the lowland colonies is more complete than it was originally because of the dying out of the forest and the spread of the staghorn fern (*Gleichenia linearis*). In this manner groups of trees are isolated from other groups of trees so that snails cannot possibly migrate. This is more especially true of lowland forms in zone II and the lower portions of zone III. In many places trees exist only in the bottom of a gulch the sides of which are covered with staghorn fern, while the tops of the intervening ridges are covered with grass. Again the trees on the side or summit of a ridge may also be surrounded by staghorn fern.

In zone III, which includes the upper part of Hosaka's (1937) Ohia Zone and all of the Cloud Zone (fig. 1, p. 3), the forest is more continuous, although in many regions large sections are covered with staghorn fern. One would expect more horizontal migration here because of the relatively larger amount of flora, greater rainfall, and the connection of the backbone ridge with the main ridges of the Koolau Range, which would afford a road for migration. On the other hand the peaks of the backbone ridge might also serve as effectual barriers. But *A. apexfulva* does not occur at the backbone

ridge. When it is collected on a ridge, the highest locality is usually a mile or more below the backbone ridge. An exception to this is area 1, which is nearer the backbone ridge. Area 115? is only an approximate locality and so cannot be considered (fig. 7, p. 194). The Nuuanu localities of area 10 are on subridges in the valley separated from the backbone ridge by a high precipice. On the other hand, although the forests are fairly continuous in zone III, migration from one ridge to another would be impeded by the gulches which contain water.

Whether there is any horizontal migration in zone III is not known. The forms in regions I, II, III, and IV, zone III, are certainly distinct from each other but have color patterns that are more similar to each other than are the color patterns in the same regions in zone II. I do not believe that the more extreme horizontal variation in zone II is entirely due to isolation which has come about in the last 50 or 100 years, because forms of *A. apexfulva* seem to colonize limited areas and to break up into different varieties or subspecies at different elevations or at short distances from an adjacent colony. This is especially true of zone II, which has less rainfall than zone III and consequently would tend to discourage migration. Nevertheless, the present-day extreme isolation and inbreeding of certain groups of genes undoubtedly accentuates the former horizontal valley-to-valley variation. The characteristic of *A. a. apexfulva* of breaking up into varieties in limited areas differs from what Crampton found (1916, 1932) in species of *Partula*, which apparently migrate into various adjacent areas and do not change color pattern in doing so.

### 3. SIZE

Table 2 (p. 15) gives the statistics of length range, mean length of shell, and number of dextral and sinistral shells found in each locality having a series of five shells or more with a length range of at least three sizes such as 18.5 mm., 19.5 mm., 20.5 mm. The means of the shells are grouped into length classes. For example, everything between 17.76 mm. and 18.25 mm. is considered 18.0 mm. and everything between 18.26 mm. and 18.75 mm., is taken to be 18.5 mm. This was also done in the paper on *A. mustelina* Mighels (Welch, 1938). In the following discussion on size variation the mean length of the shell will be referred to without needlessly repeating the words "mean length of shell."

The various localities or areas containing forms of *A. apexfulva* are grouped for convenience into 20 ridge complexes or ridge groups in order to demonstrate size variation. A ridge complex such as 3 (fig. 8, p. 195) may be a single ridge which fans out near the







terminus into four main ridges and includes not only all localities on these ridges but also all localities in valleys adjacent to or in between these ridges. Again if only one or two areas are reported from one ridge (4, 5, 12, fig. 8, p. 195) they are included with the ridge complex of the adjacent ridge, or with an area in an upper or lower portion of an adjacent ridge. With the exception of ridge complexes 1, 19, 20, which are groups of ridges, no ridge complex includes more than two main ridges, which arise from the backbone ridge of the Koolau Range. In compiling table 2, all forms from a ridge complex are grouped together. Those from localities at the lowest elevations (zones I and II) are given first and followed by forms from localities at successively higher elevations (zone III). The exact localities of most of the extinct Gulick forms are unknown, and they are placed in table 2 next to the ridge complex which probably contained them.

On figure 8 (p. 195) size variation of *A. apexfulva* in the Koolau Range is illustrated. The data given in table 2 are used for compiling the map. Where space permits, the length of the shell for each locality is plotted with the appropriate symbol. Usually there is not enough room to plot each individual locality, so that a symbol may stand for several localities or an entire area having the same shell length. The shell length of the majority of localities in an area is plotted where there is not enough room to plot the shell length of one or more localities having different shell lengths. If three lots from a single locality have three different lengths such as 17+, 18+, 19+, the middle length of 18.5 is chosen for plotting. All data from localities collected after 1932, or from localities I believe to be reliably plotted, are used in preference to less reliable material such as Wilder's and that of other collectors which has been localized by being matched with reliable material. Material which has been localized from localized data is included because in some cases it contains large series which furnish additional data as to the possibilities of size variation of a form. In some cases the localized material is represented by such small lots that it is of little statistical value.

Shells in highland localities (zone III) show as much horizontal size variation as those in lowland localities (zone II). The shells in zone I cannot be considered because of insufficient data. Little is known about zone I, and the three widely separated localities on the map in figure 8 are the only ones in zone I concerning which there are any data. They show no horizontal variation. If more were known about the location of the Gulick localities more variation would be noted in zone I. The Gulick shells came from zone I and lower zone II. Only

the Bishop Museum's portion of the Gulick collection is measured, with the exception of one Gulick lot of *A. leucozona* in the Academy of Natural Sciences of Philadelphia. This is approximately only 22 percent of the entire Gulick collection, which was broken up into 20 separate collections by Gulick. Many specimens were also traded with people all over the world by Gulick, so that 22 percent may be too high an estimate.

The Gulick material used, therefore, cannot be statistically significant, but does give an approximation of size variation of at least those series which are measured. In the region of ridge complexes 1 and 2 (table 2) 17+ shells are dominant in the Gulick lots, whereas in the region of ridge complexes 14, 15, and 19 the mean length ranges from 16+ to 17+. The 19+ forms from the region of ridge complex 15 are probably from zone II.

Zone II shows marked size variation in certain regions. Groups of ridge complexes have similar shell lengths and the change in some regions from large to small shells is abrupt. Half the ridge complexes (1, 4, 5, 7,<sup>4</sup> 8, 9, 15, 18, 19, and 20) contain mostly 18+ shells, 22 percent (ridge complexes 10, 14, 16, and 17) have mostly larger 19+ shells, and 27 percent (ridge complexes 3, 6, 11, 12, and 13) contain small 17+ shells but may also have 18+ shells. Small 16+ shells occur only in ridge complex 11.

Twenty-two percent of the ridge complexes (1, 10, 11, and 12) in zone III have small 18+ or 17+ shells. The remaining 78 percent of the ridge complexes, including number 2 (fig. 8, p. 195) have 19+ or 20+ shells, and in ridge complex 8, 21+ shells also occur. Only the uppermost localities in ridge complex 2 contain 19+ shells, the lower localities having small 18+ or 17+ shells. If size alone were considered, these lower localities would be placed in zone II. In ridge complex 3 (fig. 8, p. 195) what appears to be the highest area contains 18+ shells. Actually this area (area 12, fig. 8) is on the lower portion of a small spur ridge in ridge complex 3 and is at a lower elevation than the other localities. Ridge complex 7 also has 18+ shells in zone III (area 31, table 2). This may be due to the small number of shells measured; possibly if a larger series were obtained, the mean length would be greater.

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<sup>4</sup>Area 27A?, the lowest area in ridge complex 7, has a mean length of 18.77 mm. and is therefore represented in figure 8 by the symbol for the 19+ class shells. However, it really is very close to the 18.5 class and could be considered an 18+ area.

## B. VERTICAL VARIATION

## I. EMBRYONIC WHORLS

No vertical variation in the color of the embryonic whorls occurs in regions I, II, IIa (fig. 7, p. 194). Vertical variation occurs between regions IIIa and the portion of region III immediately above IIIa, and on the North-South Kaukonahua Ridge between regions IV and IIb. The lower regions have shells with unicolored embryonic whorls (region IV) or with embryonic whorls that are intermediate between the bicolored and unicolored condition (region IIIa). The upper regions III and IIb on the other hand have shells with bicolored embryonic whorls (fig. 7, p. 194).

In area 77, between regions IV and IIb, shells of *A. a. tuberosus* var. 3 have either unicolored or bicolored embryonic whorls. In the Gulick collection specimens of *A. a. polymorpha* have either bicolored or unicolored embryonic whorls. This may indicate that at a low elevation (zone I) in the region of Waiawa and Kipapa Gulch shells with unicolored embryonic whorls existed below the present-day forms with bicolored embryonic whorls in zone II of region III.

Region IV contains only shells with unicolored embryonic whorls but northwest of North Kaukonahua Stream to Opaepala Gulch in the lowest areas (areas 85, 86, 89, 90, 91??, 92, 93, 95, 96, 106, 107, 109, fig. 5a, p. 105), the shells have dark embryonic whorls which are some shade of brownish yellow such as ochraceous tawny or buckthorn brown. The upper localities have lighter embryonic whorls with such colors as white, light buff, or pale pinkish buff. An exception to this rule is area 88, which contains shells with darker embryonic whorls than lower area 87. Area 97 of Opaepala Gulch (ridge complex 18, fig. 8, p. 195) has shells with darker embryonic whorls than those of area 99 above it. But area 97A??, which is below area 97, has shells with white embryonic whorls. So that in the region of Opaepala and Kawailoa Gulch three distinct types of embryonic whorls occur: Highland white or buff, lowland brownish, and finally white in the extreme lowland shells. Northwest of Kawailoa Gulch no vertical variation is noted in the color of the embryonic whorls in shells found today.

## 2. COLOR PATTERN OF THE POSTEMBRYONIC WHORLS

The postembryonic whorls show more vertical variation than the embryonic whorls. At different elevations along a ridge different colonies or areas with distinct color patterns are encountered. The

vertical variation between two areas is usually more marked than the horizontal variation. In studying the patterns of any area or locality in relation to other forms, not only must the shells in areas on adjacent ridges on either side be considered, but also those above and below the area on the same ridge.

The color patterns of the Koolau Range can be divided into light and dark. The light patterns are: 1, white strongly banded with reddish brown; 2, white lightly banded or lined with reddish brown; 3, white banded with yellow or tan; 4, pink or flesh color, which may be banded with white. The dark color patterns are: 1, gray mixed with pink; 2, brown; 3, grayish brown or gray; 4, reddish brown; 5, reddish brown banded with yellow; 6, yellowish or tan; 7, gray mixed with yellow.

The division of color patterns into light and dark forms in the Koolau Range, while very close to the division of patterns between zones II and III, is not the same. A dotted line has been drawn (fig. 7, p. 194) showing the boundary between highland light color patterns, usually present in zone III, and lowland darker patterns not dominantly banded with white, which exist below the line in zone II and lower zone III. With the exception of areas 30 and 33 (fig. 7, p. 194), which contain dominantly yellow patterns, all forms above the dotted line are white forms banded with various colors, usually reddish brown or yellow. In all areas below the dotted line, with the exception of area 97A??,<sup>5</sup> not only are the shells darker in color but also the patterns are axially streaked. Area 70, below the dotted line, has white color patterns which are distinct from the highland forms in being tinted with gray and in not having the white ground color found on shells above the dotted line. Pink shells from lowland areas (37?, 83b??) differ from pink shells found above the dotted line in not being banded with white and in lacking white color patterns.

Therefore, the color pattern of shells coming from areas of high humidity (most of zone III) tends to be dominantly white and banded, while shells with darker patterns which are banded and streaked occur in dryer situations (lower zone III, zone II, and zone I). Although banded patterns are not characteristic of highland or lowland forms, streaked patterns with the exception of area 97A??, seem to be characteristic of shells inhabiting dry situations. This cor-

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<sup>5</sup> Area 97A?? contains white color forms lightly lined and banded and not markedly axially streaked. This locality is an exception to the general rule concerning the color pattern of lowland color forms.



relation between pattern and elevation in *A. aperfulva* was noted by Pilsbry and Cooke (1912-1914) and Welch (1938a). No correlation exists between a particular pattern and a definite altitude.

The shells of area 1 (fig. 8, p. 195) are near the backbone ridge and would be expected to contain white shells and be part of zone III. However, area 1 contains lowland dark streaked gray forms although it is at a higher elevation than area 3, where white shells occur. As regards moisture conditions, area 1 is found to be in a section of relatively low humidity as compared with most localities to the northwest in zone III. Northeast of Nuuanu near the backbone ridge the rainfall decreases the farther one goes to the northeast (compare Luakaha (upper) with Makapuu, table 1, p. 10).

Region I, northwest of Palolo, shows less variation than the other regions. This is probably due to the fact that the lowland localities are all wiped out and only the upper less variable forms exist today. However, from what is known of shells collected by Gulick and older collectors in the region of Nuuanu-Kalihi, there existed a number of small dark-colored races of shells below the present-day white races. Area 15 is the only area in the Nuuanu-Kalihi region with markedly dark color patterns.

Little vertical variation is shown in the Halawa section of region II. Area 21 has white shells, above which in areas 22 and 23 the dominant pattern is white but contains yellowish banded and lined forms which are darker than those found in area 21. Two of these rarer darker patterns from area 23 are shown on plate 1, figures 27 and 28.

The shells in area 26 are brown, banded with white, and are lighter in color than those higher up the ridge, which are yellow banded with brown in area 25. Above area 25, the usual color pattern is white. North of Kalauao to Waimano, the lowland areas have shells with brown patterns grading into yellow at a higher elevation and finally, in area 31, into white. In Waimano, in area 34, brown patterns occur which also grade to yellow and finally to white in the upper areas. But below area 34, in area 35, reddish-brown patterns are found, and these occur also in areas 44 and 50. Above these last two areas the shells of the upper areas have patterns that contain more and more white and are less heavily banded with reddish brown.

North of Waimano, in regions III, IIIa, and IV, the predominant lowland patterns, zone II and lower zone III, are brown or gray with here and there an area of reddish-brown, yellow, or pink shells. Above these in zone III the color patterns are all white. Region IV is the section of the Koolau Range which shows maximum vertical

differentiation. The contrast between lowland streaked and highland banded patterns is very marked. On some ridges as many as 7 or 8 distinct color races are found (see pl. 2, figs. 24-30; pl. 3, figs. 1-8, 12-18, for examples of forms occurring on three ridge complexes).

North of Kawaihoa Gulch no particular zoning is known to occur today in ridge complex 19. But in Gulick's day there must have been a division between *A. a. napus* and the darker reddish-brown forms that occur today in areas III, II2, II3, II4.

### 3. SIZE

Thirteen ridge complexes (2-6, 8-9, 13-15, 17, 18, and 20, fig. 8, p. 195) show size increase in the majority of localities with increase of elevation. The smaller lowland shells, with the exception of area 2, are in zones I and II and are usually 17+ or 18+ mm., with here and there a locality with 19+ shells. In area 2 all forms are in zone III, but all the lowest localities have small 18+ or 17+ shells, similar in size to those usually found in zone II, while the highest locality contains 19+ shells. In all the remaining 12 ridge complexes showing size increase in zone III, the shells are 19+ or 20+ mm. Although there is a contrast between zones II and III the increase in size is not a gradual one. The highest localities do not contain the largest shells. Northwest of ridge complex 7, 19+ shells occur above 20+ shells in many localities. In ridge complex 8, 20+ shells occur above 21+ shells. Ridge complex 3, area 12 (table 2), has 18+ shells and appears on figure 8 (p. 195) to be at a higher elevation than the 19+ shells. However, the shells were collected on a small spur ridge of ridge complex 3, probably at a lower elevation in Nuuanu than the 19+ shells. The exact extent of the locality is uncertain.

The 18+ sinistral shells from area 62?, ridge complex 14 (table 2), are reported from the same locality as the larger 19+ dextral shells, and are separated because of the size difference. If both dextrals and sinistrals are lumped together, the mean length is 18.0 mm. The locality was plotted 13 years after being collected and probably represents two localities, one of dextral and one of sinistral shells. On figure 8, ridge complex 14, 18+ shells are plotted above 19+ shells, which may be an error. Whether the dextral or sinistral shells occur in separate localities, or one above the other, is of no great importance. The small 18+ shells are of interest because they are another exception to the general trend.

Out of the seven ridge complexes not showing altitudinal size variation, two can be disregarded. One of these, ridge complex 19, is

all in zone II; the other, ridge complex 10, is represented by only one locality in zone III, which contains only five specimens. The remaining five ridge complexes show no marked variation in the majority of localities between zones II and III. Ridge complex 1 contains only 18+ shells, regardless of altitude. If the Gulick shells from this general region, probably zone I and lower zone II, are compared with present-day forms, size variation can be noted. The lower Gulick forms are 16+ or 17+, shells. However, if all the Gulick shells in institutions outside of the Bishop Museum collection were measured and considered together, the mean length might be greater, probably 18+ instead of 17+. The highest locality in ridge complex 7 (area 31, table 2, p. 15) has 18+ shells, while the lowest locality (area 27A?) has shells with a mean length of 18.77 mm., or 19+ shells. In between these localities, 19+ and 20+ shells occur.

The most remarkable exceptions to altitudinal size increase are ridge complexes 11 and 12, which have small 17+ shells occupying the majority of localities in both zones II and III. In ridge complex 11, zone III, 16+ shells also occur. Localities of 18+ shells are found here and there in both zones II and III in both these ridge complexes.

As with *A. mustelina* (Welch, 1938), no clear-cut correlation can be drawn between increase of moisture and size variation. The highest localities in ridge complex 1 near the backbone ridge range in elevation from 1,650-2,000 feet, while those in ridge complex 2 range from 1,150-1,500 feet. However, the rainfall in upper ridge complex 2 is undoubtedly greater than in upper ridge complex 1, for although there are no rain-gage stations in this region, south of Nuuanu and Manoa the backbone ridge undoubtedly receives less rainfall (compare Luakaha (upper) with Makapuu, table 1, p. 10), so that in this case a correlation can be drawn between increase of size and increase of moisture. In a similar manner the localities in area 8, which is a much dryer section of Nuuanu Valley than area 10, have smaller shells than the upper locality even though the elevation of both areas is about the same (compare Luakaha upper and Luakaha lower, table 1, p. 10). While a correlation can be drawn between an increase of size with an increase in moisture conditions in ridge complexes 1 and 2, it is not possible on the same basis to explain the small shells of ridge complexes 11 and 12, zone III, or the larger 19+ shells of ridge complexes 7, 16, and 17, zone II.

Even though exceptions occur at random, 65 percent of the ridge complexes show a size change between zone II and III. A correla-

tion, then, can be drawn in the majority of ridge complexes between increase of size with increase of moisture and lower temperature. This is the reverse of what was found for *A. mustelina*, which species shows a correlation between decrease of size and increase of moisture. Therefore, these two different species react very differently to similar environmental conditions, the reaction probably depending not only on the genetic make-up of the individual but also on the influence of the environment on the hereditary factors.

#### 4. SHAPE

If the usual form of the shell from each area is considered and the ratio of the length to the greater diameter is obtained, the usual form of the shell is found to vary at random. Only in ridge complex 15 is any vertical variation shown; here the lower areas contain narrower shells than the highland areas. This general condition is similar to that found in the case of *A. mustelina* (Welch, 1938). In most areas in the Waianae Mountains *A. mustelina* showed no vertical variation. Only in the northern section of the mountains is the shape of the shell found to change from elongate lowland to more squat highland forms.

#### C. VARIATION WITHIN A LOCALITY OR AREA

##### I. COLOR PATTERN OF EMBRYONIC AND POSTEMBRYONIC WHORLS

Each subspecies in a given locality has a range of color patterns from light to dark. The dark color patterns of shells from some areas in zone III in regions I and II are often very different from the usual white color form of the shell. In area 8 (pl. 4, fig. 15*b*), area 12 (pl. 4, fig. 20*b*), area 11 (pl. 5, fig. 2*b*), area 10 (pl. 5, fig. 1*a*), and area 46 (pl. 7, fig. 14*a*) dark reddish-brown forms occur which would never have been expected in an area of white shells. One of the most striking examples of this occurrence of two widely differing color patterns from the same locality is to be seen in the region of the North Kaukonahua area 103 of *A. a. roseipicta* var. 1. The dominant color pattern (pl. 3, fig. 8) is a pinkish one banded with white, and the other color patterns are white ones banded with pink. With these patterns, a few rare dark gray color forms occur (pl. 12, fig. 6) which are strikingly different. The same thing occurs in area 105. In area 100? the strikingly banded patterns of *A. a. aloha* var. 1 may be an example of the same thing, but in this locality the patterns are not only different but show a series of variants which may indicate a separate area containing special color patterns.

## 2. FORM

A considerable amount of trouble has been taken to show the range of form variation within each area. The extreme narrow and obese forms of the shell are generally figured for each form and the measurements given in the text. For example, various forms of *A. a. turgida* have been figured on plate 6. The extreme obese form of the shell (pl. 6, fig. 4a) looks very different from the narrow form of the shell. The spire may be concave in outline (pl. 6, fig. 4e) or straight in outline (pl. 6, fig. 5). The contrast between the narrow (pl. 5, fig. 17) and the obese form (pl. 5, fig. 17a) of *A. a. bruneola* is enough to lead to the consideration of the specimens, disregarding color, as two different forms. In like manner specimens of *A. a. parvicolor* (pl. 6, figs. 15, 15a) also show marked variation, as do many other subspecies. Just as with color pattern, the shape and size of the shell cannot be used as a criterion in determining a species, unless a series of forms are available so that something is known about the range of variation.

## D. SIZE VARIATION IN THE SAME COLONY OVER A PERIOD OF YEARS

There is little information on this question. *A. a. rubidipicta* (area 11, ridge complex 3) collected from 1921 to 1929 shows little variation over a period of years (see table 2, p. 15). *A. a. turgida* (area 35, ridge complex 8) collected from locality 202b from 1920 to 1934 shows no variation in the mean length of the shell over a period of 14 years. However, a lot collected in 1913 (table 2) is smaller than the lots collected in 1920 to 1934. This difference in size of the 1913 lot might be interpreted to be a size change or evolutionary change occurring in a period of 7 years, but I believe it is more likely the result of an error due to the small number of shells or to the collecting of the shells in a locality slightly different from, or lower than, that where later collections were made.

As in the case of *A. mustelina* Mighels (Welch, 1938, p. 142), I do not believe any evolutionary change has brought about a difference in the size of shells of *A. apexfulva* collected 20 years ago and those collected in the same locality today. This differs from Crampton's (1916, 1932) findings in his study of *Partula* of the Society Islands.

## E. DEXTRALITY AND SINISTRALITY

No order is found in the occurrence of dextral and sinistral forms either horizontally or vertically. Ridge complexes 15-20 are domi-



nantly dextral, while ridge complexes 1-14 contain both dextral and sinistral shells with the exception of ridge complexes 2 and 4, which have only sinistral forms.

#### F. THE EFFECT OF THE HABITAT ON SUBSPECIATION

Gulick (1905) does not believe that natural selection due to external conditions explains the diversity of species in *Achatinella*. He points out that climate, soil, and vegetation are essentially the same from valley to valley. He discounts the effect of differences in the amount of rainfall in a locality on speciation, because forms from the south-east slope of the Koolau Range show more divergency among themselves than those on opposite sides of the Koolau Range, even though the rainfall is greater on the northwestern or windward slope than on the leeward slope. Gulick collected most of his material at a low elevation below 1,500 feet. He had no material that showed any possible variation between a lowland dry locality and a highland more humid locality in the same valley or on the same ridge. The diversity of forms on opposite sides of the Koolau Range is certainly as great as, if not greater than, that found between forms on the same side of the mountains.

Crampton (1932, p. 208), in his study of *Partula* from the Island of Moorea, states:

With reference to the problem of the possible effects of the environment upon structural or other qualities the only conclusion warranted by the facts is that congenital factors are solely responsible for the diversities exhibited by the several varieties, by the numerous colonies, and by the individual components of the colonies.

Dobzhansky (1937, p. 136) believes that while it is difficult to prove that a given trait is not, or has not been, influenced by adaptation to the environment, nevertheless the facts given by Crampton and Gulick are explainable on the assumption that racial differences are merely due to random mutations and to random changes of gene frequencies in isolated populations. In discussing Wright's papers on evolution Dobzhansky (1937, p. 134) explains how species may be differentiated into subspecies. Such an explanation applied to *A. apexfulva* would satisfactorily account for valley-to-valley variation. However, it does not explain why there is a definite vertical change in color pattern along a definite line such as the dotted line in figure 7 which divides highland dominantly white color patterns from lowland dark color patterns. If variation is purely a matter of the random combination of genes and mutations within a locality, both highland

and lowland localities have an equal chance of having dark or light color patterns and should occur in both areas at random. Possibly, then, other factors such as difference in moisture conditions, temperature, differences between a highland and lowland flora, and various other ecological factors are playing a role. The highland set of external factors may be favorable to white color patterns, while the lowland ones favor the survival of dark patterns.

These data indicate that subspeciation within the species *A. apexfulva* is due both to the effects of random variation in partly isolated populations and to selective factors in the environment.

#### SUMMARY

1. The various forms of *A. apexfulva* are organized into subspecies. New subspecies to the number of 43 are recognized from a total of 78 forms.

#### HORIZONTAL VARIATION

2. The embryonic whorls may be either bicolored or unicolored. Shells with bicolored embryonic whorls occur in regions I, III, and IIIb; those with unicolored ones occur in regions II and IV. Regions Ia, IIa, and IIIa have embryonic whorls which are intermediate between the bicolored and the unicolored condition.

3. The color pattern of the postembryonic whorls shows marked differentiation between regions I, II, III, and IV, and less variation within each region. More horizontal differentiation occurs in zone II than in zone III. No horizontal migration is noted of one form invading the territory of another, because *A. apexfulva*, like *A. mustelina* (Welch, 1938), tends to break up into subspecies at different elevations and at short distances away from a given colony.

4. Highland forms occurring in zone III show as much horizontal size variation as lowland forms in zone II. Half the ridge complexes in zone II have 18+ shells, 22 percent have 19+ shells, and 27 percent have a mixture of 18+, 17+, and 16+, shells. In zone III 22 percent of the ridge complexes have 18+ or 17+ shells, while 78 percent have 19+, 20+, or 21+ shells.

#### VERTICAL VARIATION

5. Vertical variation occurs in the color of the embryonic whorls between regions IIIa and III, and between regions IV and IIIb. Regions III and IIIb have shells with bicolored embryonic whorls,

region IV has shells with unicolored embryonic whorls, and region IIIa has embryonic whorls intermediate between the bicolored and unicolored condition. In ridge complex 18, area 97A?? (fig. 8, p. 195) has shells with white embryonic whorls; above this area (area 97) shells with yellowish-brown embryonic whorls are found; and in areas 98 and 99 at a still higher elevation shells with lighter buff embryonic whorls occur.

6. The color pattern of the postembryonic whorls varies at different elevations, and this variation is usually more marked than the horizontal variation. Shells from areas having a high rainfall tend to be white and to have banded patterns; those occurring in dryer situations (lower zone III, zone II, and I) tend to have darker patterns which are banded and streaked. The region of maximum vertical variation is region IV.

7. Out of 20 ridge complexes, 13 show size increase with increase of altitude between lower zone II and higher zone III. The remaining ridge complexes are exceptions to the general trend. Although the correlation is not so clear-cut as for *A. mustelina*, a definite tendency toward size increase with increase of moisture and lower temperature exists in *A. apexfulva*, just the reverse of the correlation for *A. mustelina*.

#### FORM AND COLOR

8. The shape of the shell varies at random both vertically and horizontally.

9. No order in the distribution of dextral and sinistral shells is ascertained.

10. Color variation within a locality is often very extensive. This makes it necessary to study large series in order to ascertain whether a form is a distinct race or merely a color pattern of a known subspecies. The same color pattern may occur again in a number of widely separated localities. The embryonic whorls may be unicolored or bicolored in the same locality.

11. Form varies a great deal within a locality. A subspecies may have narrow or obese shells. The spire may be straight, concave, or convex in outline. Therefore, form is no criterion for the naming of a species or subspecies until the range of variations of a series of specimens is studied.

12. Over a period of years no size variation was noted in shells from a definite locality. However, little data was available on the subject.

## SUBSPECIATION

13. Subspeciation in *A. apexfulva* is believed to be caused by both the effects of random variation in partly isolated populations and selective factors of environment.

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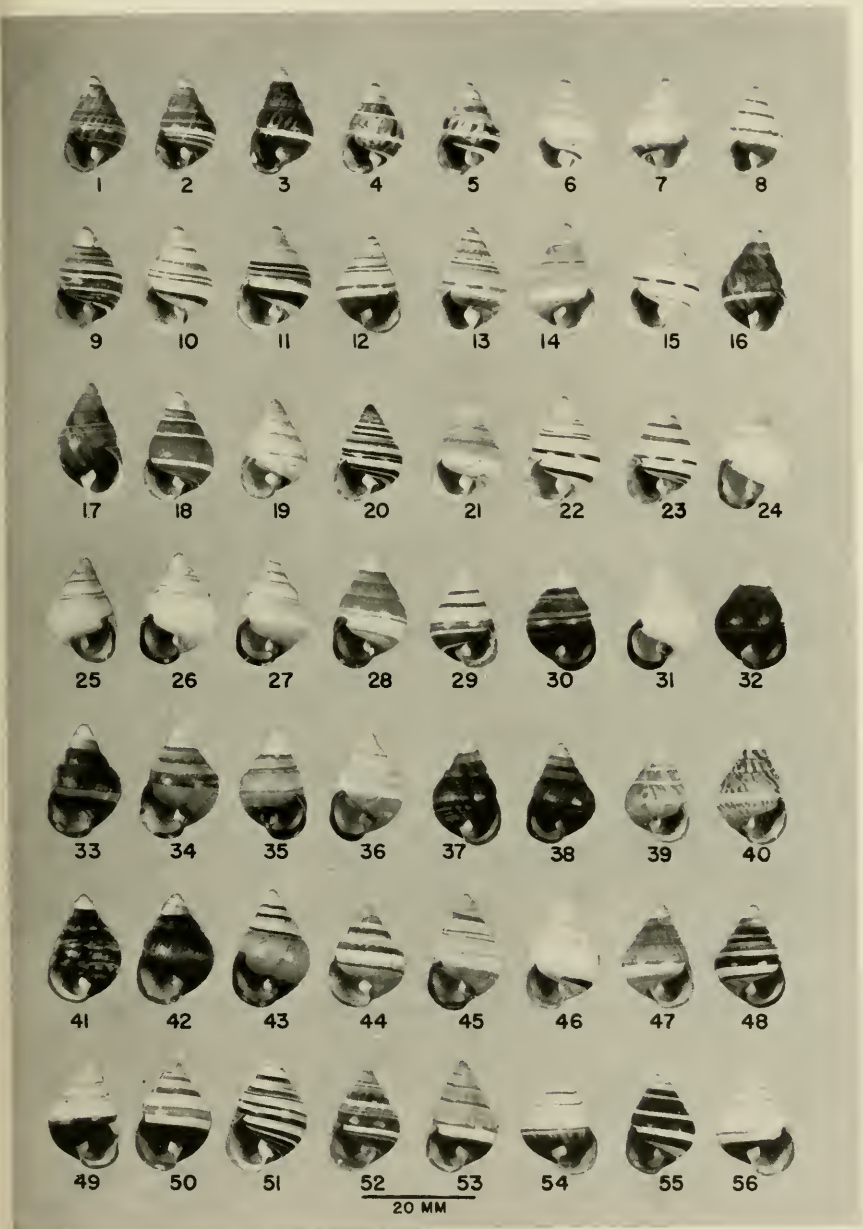
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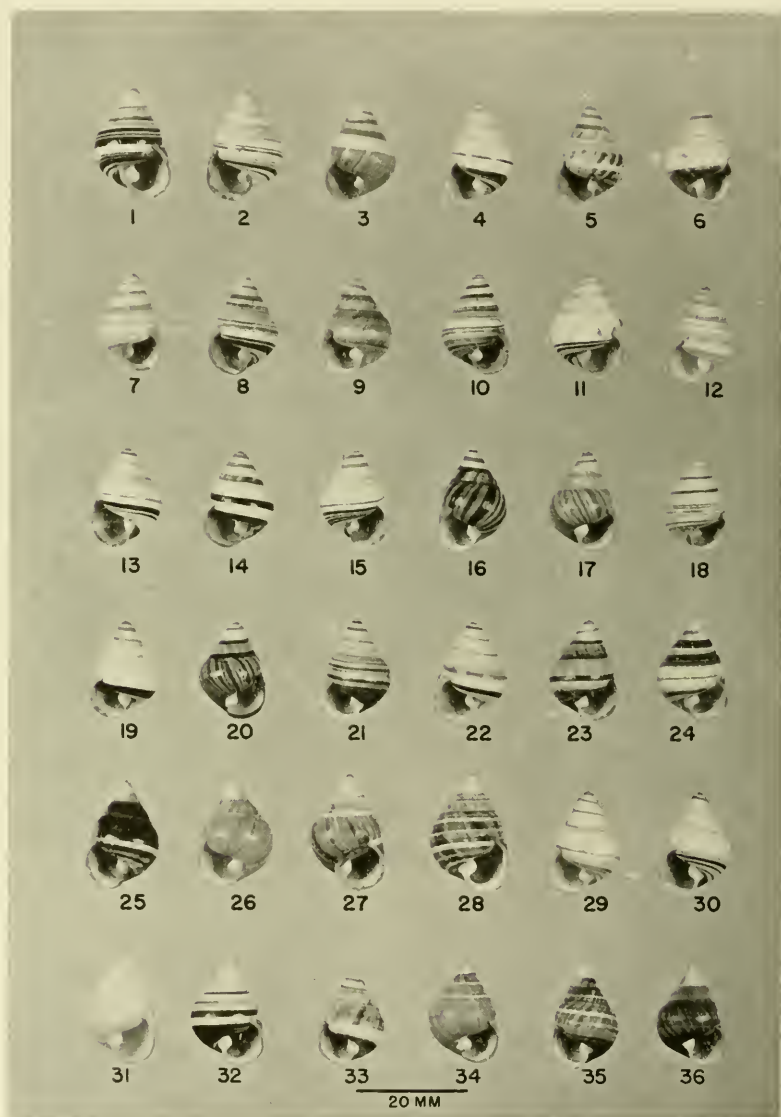
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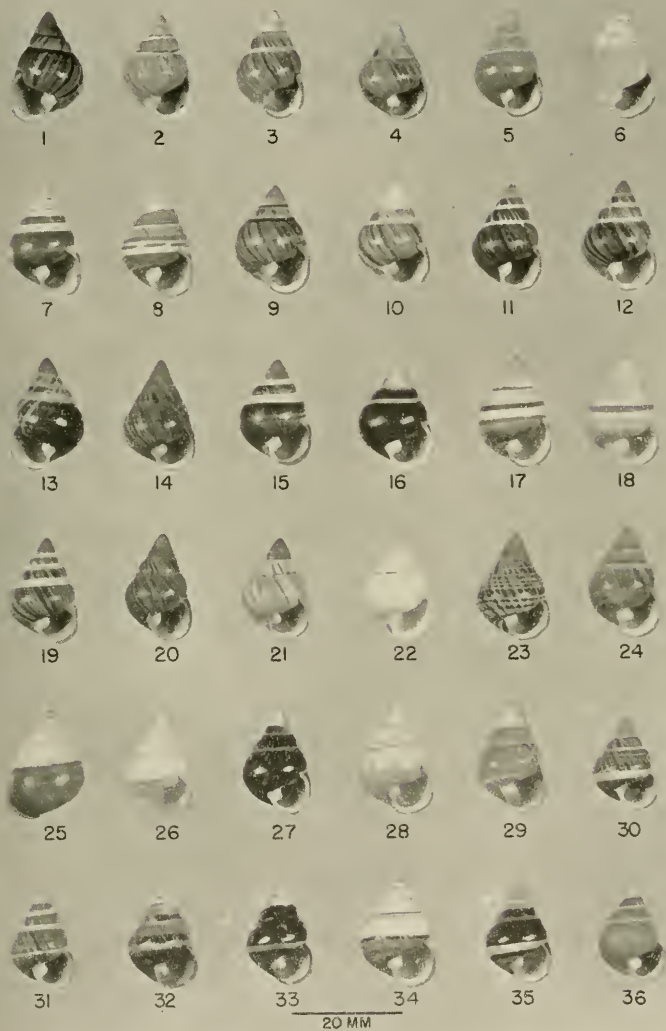


SUBSPECIES OF *ACHATINELLA APEXFULVA*  
(For explanation, see pages 208-210.)



SUBSPECIES OF *ACHATINELLA APEXFULVA*

(For explanation, see pages 211-212.)



SUBSPECIES OF *ACHATINELLA APEXFULVA*  
(For explanation, see pages 212-213.)

SUBSPECIES OF *ACHATINELLA APEXFULVA*

(For explanation, see pages 213-214.)

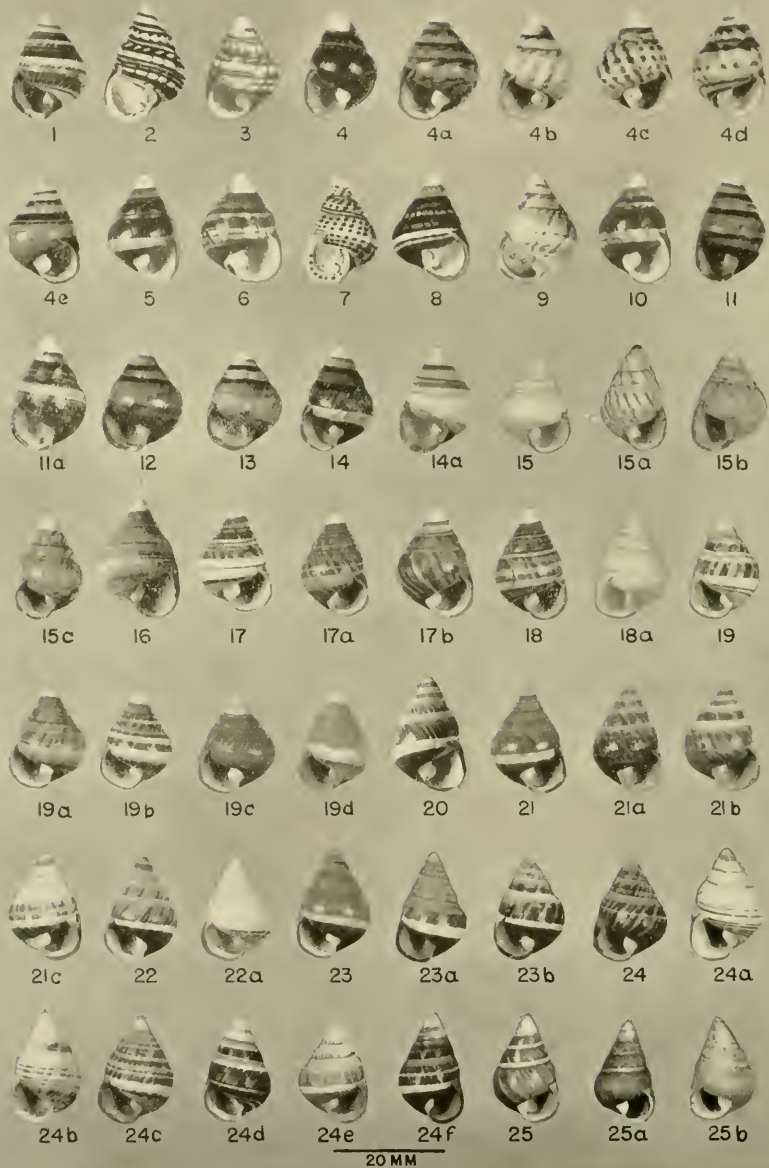




SUBSPECIES OF *ACHATINELLA APEXFULVA*

(For explanation, see pages 214-215.)



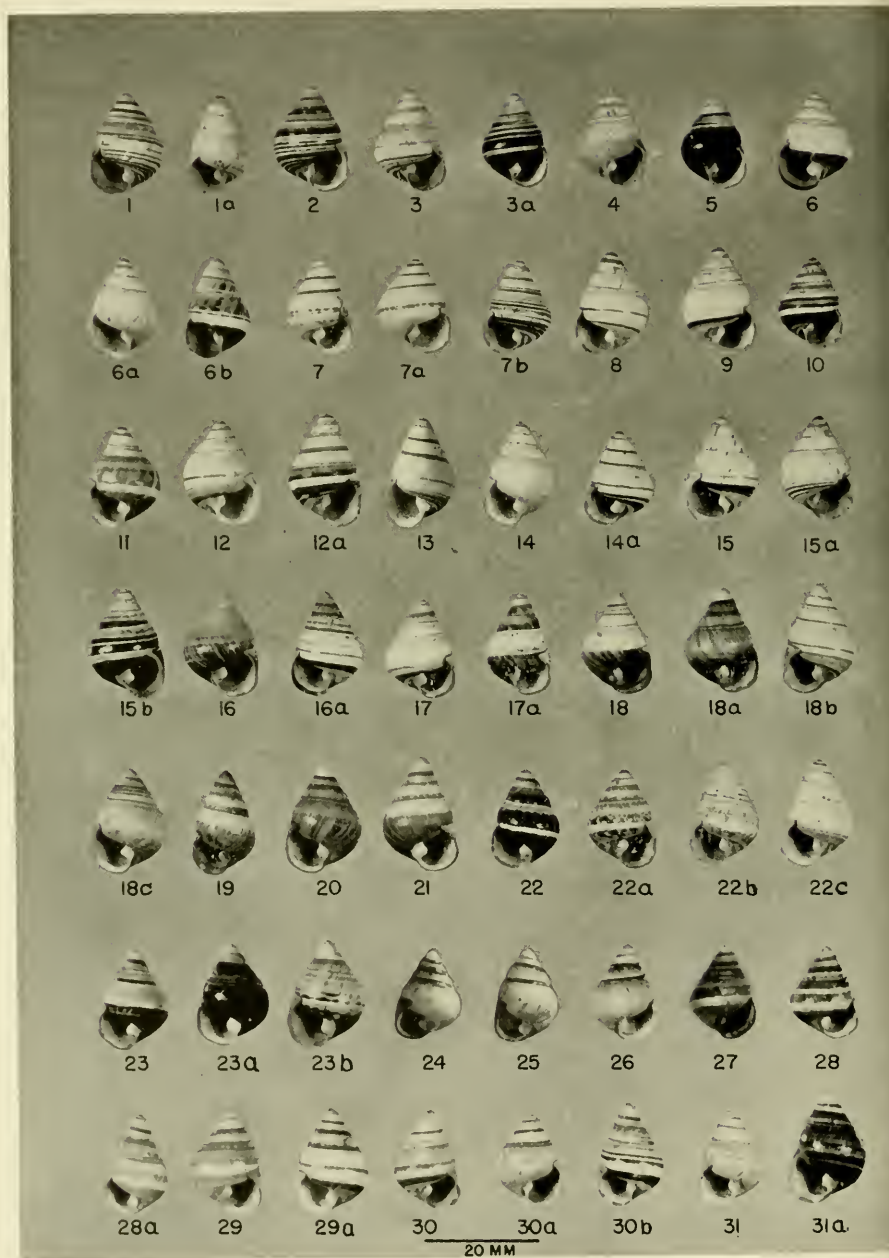
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(For explanation, see page 216.)

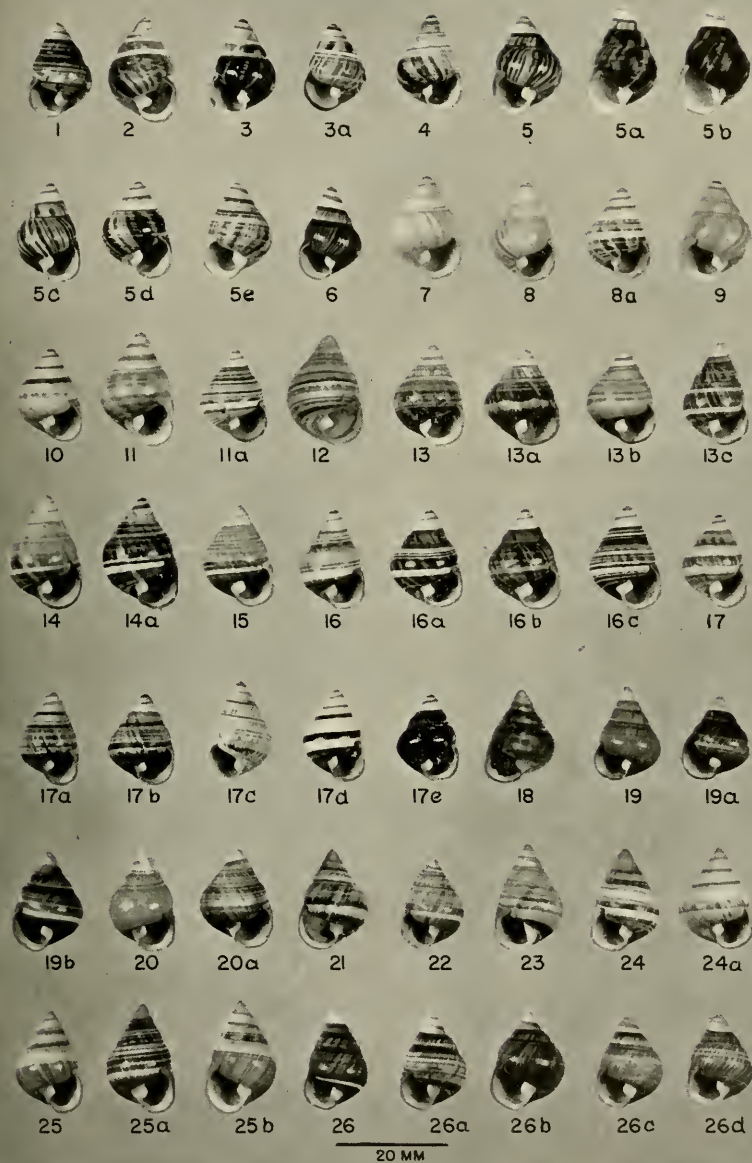


SUBSPECIES OF *ACHATINELLA APEXFULVA*

(For explanation, see page 217.)



SUBSPECIES OF *ACHATINELLA APEXFULVA*  
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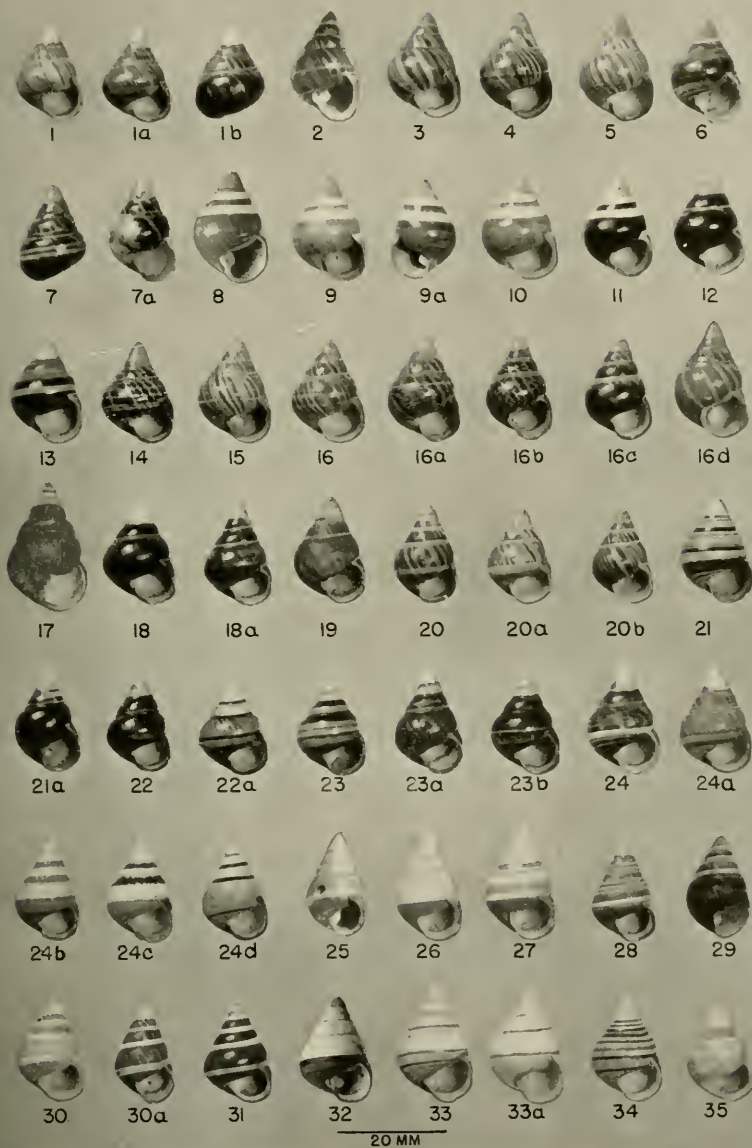
(For explanation, see page 219.)



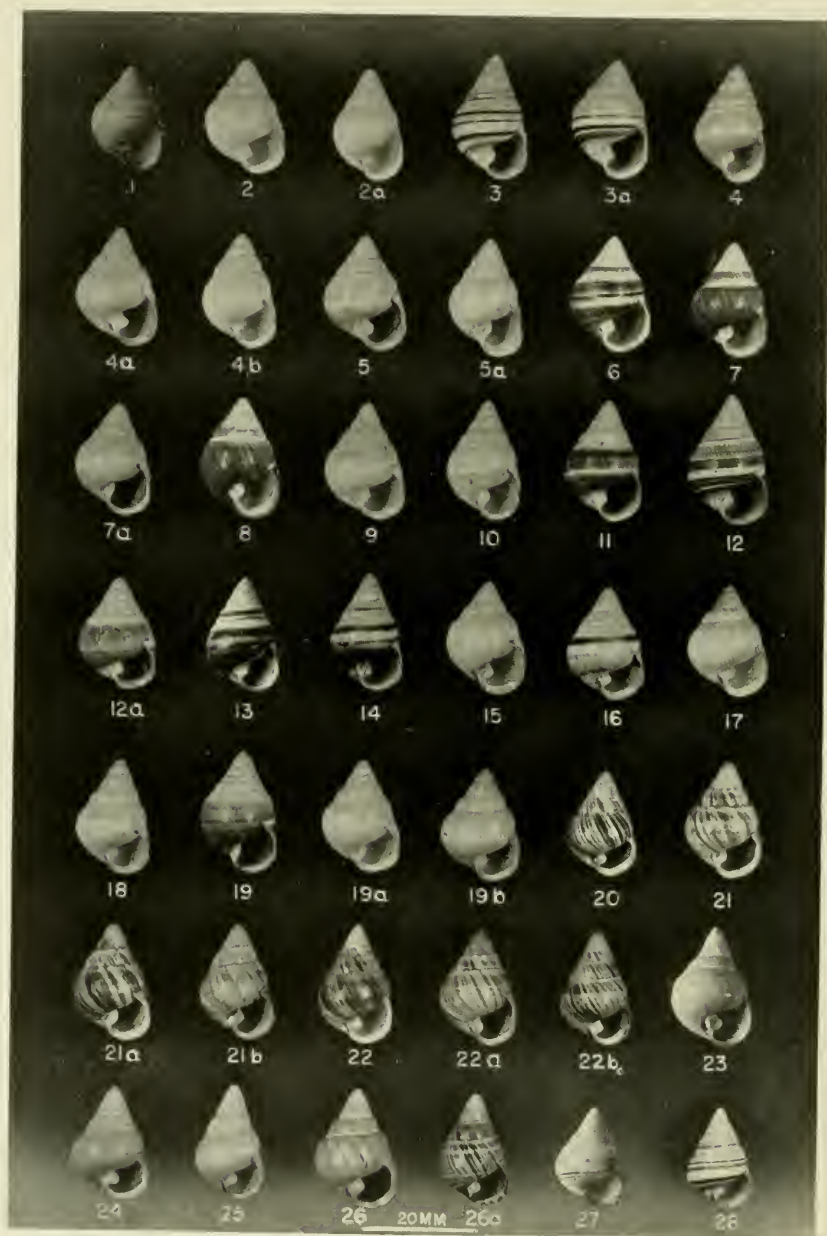


SUBSPECIES OF *ACHATINELLA APEXFULVA*  
(For explanation, see page 220.)



SUBSPECIES OF *ACHATINELLA APEXFULVA*

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## INTRODUCTION

An insect is preeminently a miniature machine; its mechanical elements are the skeleton and the muscles. The skeletal structure, therefore, cannot be fully understood without observing its correlation with the muscular system and the part it plays in the body mechanisms. And yet, almost our entire code of insect anatomy has been built up on a study of the external pattern of the skeleton, done in about the same way that a casual student of geography studies a map of the world. The results of our charting of the surface structure, however, have not been so far wrong as might be supposed, because all the lines that are commonly said to "divide" the insect exoskeleton into sclerites have a mechanical significance, and many of them are of fundamental importance in the insect mechanism. The common mistake is the assumption that the sclerites themselves are the fundamental elements of the skeletal organization, that the sclerites have been handed down from a remote ancestor, and that the primitive sclerite pattern has been somehow altered without essential changes to fit the varying needs of modern insects.

The diversifications of the insect skeleton are far too extensive to be reduced to any one formula, but in general it may be said that sclerites which are defined by grooves, or "sutures," in a continuously sclerotized region are subdivisions of the skeleton that are merely incidental to the formation of internal strengthening ridges, while

sclerites isolated in otherwise membranous areas are themselves functional units. Most sclerites, therefore, instead of being primitive elements of the exoskeleton, are more probably recent developments accompanying the evolution of skeletal mechanisms.

With regard to the homology of sclerotized areas the question often arises as to whether or not an area of sclerotization represents necessarily a primary morphological area. As, for example, if a so-called pleural plate that ordinarily is confined to the side of the thorax is found in some species to be continued down upon the venter, are we to assume that the original pleural integument has accompanied the sclerotic extension into the venter at the expense of the primitive sternal integument, or is it merely that the physiological process of cuticular sclerotization has spread beyond the usual limits? Until this question can be answered, confusing problems in nomenclature will always intrude themselves into practical anatomical descriptions.

A similar question concerns the significance or morphological value of muscle attachments. Do muscle attachments necessarily imply homology in the skeletal parts, or can muscles shift their attachments from one place to another? In answer to this question there is abundant evidence that the so-called insertion points of muscles seldom show radical changes, while, on the other hand, the points of origin may be at widely different places on the skeleton in different species. Evidence of homology, therefore, is pretty sound when based on the working end of the muscle, though the work performed by the muscle may be entirely different in two species by reason of a change in the position of the muscle or some alteration in the skeletal mechanism. We do not know, however, whether a muscle arising at different places in two species has *migrated* during the evolution of one species or the other, or whether a muscle, during its formative stage of development, may *evoke* an entirely new attachment on the body wall by some hormonal effect at the point where its end comes in contact with the epidermis.

The musculature of the head and the feeding organs appears to be more nearly standardized than that of any other part of the insect, regardless of the great variation in structure and function of the mouth parts. The muscles of the thorax, the legs, the abdomen, and the ovipositor conform fairly well with an underlying plan, but the number of muscles is far from constant. The musculature of the male genitalia, however, shows no prevailing pattern and may be entirely different in different orders of insects. The contrast between the stability of the mouth part musculature and the variable nature

of the male genital musculature may mean that the external genital organs of male insects, as compared with the mouth parts, are new structures having no antecedents going far back in hexapod ancestry. The wings are examples of new structures with a highly consistent musculature, but the wing mechanism has been adapted to the thoracic musculature present before wings were developed.

A study of insect mechanisms, aside from its morphological value, is important from the standpoint of understanding the functional activities of insects, and opens a wide field in entomological research to students who may be mechanically inclined. Insect mechanisms have little resemblance to man-made machines, for one reason, because animals cannot have anatomical wheels, and for another, because the insect cuticle has properties of flexibility and elasticity that react with muscle tension to produce movements that cannot be imitated in the usual rigid materials of human workmanship. The insect machine, therefore, depends on the use of levers and springs and hydraulic apparatus, but still it is not impossible that inventors might get a few hints from its study.

## I. THE HEAD AND THE FEEDING APPARATUS

The hymenopterous head and the organs of feeding, by comparison with these parts in such orders as Lepidoptera, Diptera, and Hemiptera, show relatively little deviation from the generalized plan of structure in fundamental ways; but, on the other hand, they present numerous minor specializations and many finely adjusted mechanical alterations by which they are adapted to methods of feeding and to nonfeeding uses not found in any of the other insects. The structures directly concerned with the intake of food in the bee include the labrum, a large preoral epipharyngeal lobe on the under surface of the clypeus, the mandibles, a maxillo-labial complex, or proboscis, the mouth, and an internal sucking pump. Intimately associated with the ingestive organs, moreover, is a salivary ejection pump, or syringe, for the discharge of the saliva from the salivary duct. The hypopharynx does not appear as an independent organ in the bee; its distal part is incorporated into the base of the labium and its proximal part forms the floor of the mouth.

The natural food materials of the bee are principally pollen and nectar, both being carried to the hive for storage, where the nectar is converted into honey. The eating of pollen involves little more than a use of the mandibles in the primitive manner of biting and chewing insects, and modification of the mandibles in the bee pertain chiefly

to the worker caste, in which the jaws serve as tools for handling wax. The ingestion of nectar from the depths of flower corollas or of honey from the cells of the comb, on the other hand, necessitates a special apparatus for reaching the liquid and for drawing it up to the mouth. Hence the principal structural modifications of the feeding apparatus affect those parts that contribute to the formation of the proboscis and the sucking pump. These same organs are able to function also in reverse for the regurgitation of nectar and honey. The principal "new" feature in the mouth parts of the bee is the salivary channel of the tongue, but this channel is probably only an elaboration of a groove along the line of union of the glossae. Finally, the need of having the proboscis out of the way when comb-building is in progress, or when the mandibles are otherwise in use, has been met by adaptations in the free parts of the proboscis that enable the latter to be folded and temporarily stored in a receptive cavity on the back of the head, from which the parts can be again extended and reassembled for functional purposes.

The so-called proboscis of the bee is hardly to be termed an "organ," since as a functional unit it is improvised when the bee would feed on liquids by bringing together the various free parts of the maxillae and the labium (fig. 3 A) in such a way as to form a tube (C) through which nectar, honey, or water may be drawn up to the mouth. When not in use the parts are disassembled and folded back behind the head (fig. 3 B), where they are held in place by the mandibles (*Md*) clasped beneath them. The major parts of the maxillae and labium are adapted in form to the roles they play in the functional position; the flexing mechanism depends on smaller modifications and minute adjustments between the skeletal elements and certain muscles. All the specialized movements involved in the operation of the proboscis of the bee, however, are produced by muscles that can readily be identified with the usual muscles of the maxillae and the labium in generalized insects.

The adjustable components of the proboscis are the broad, bladelike galeal lobes of the maxillae (fig. 3 A, *Ga*), the long labial palpi (*LbPlp*), and the slender median tongue formed of the united glossae (*Gls*). When these elements are assembled to form a tube, the galeae and the palpi are brought alongside the tongue and, with the last, enclose a temporary channel. The wide galeae (C, *Ga*) form the sides of the tube and overlap each other above the tongue to form also the roof; the labial palpi (*LbPlp*) lie beneath the galeae and close the tube below by underlapping the tongue, while marginal fringes of hairs on the galeae and palpi prevent leakage between



the approximated parts. The pointed ends of the galeae converge over the protruding distal part of the tongue (fig. 3 C), but the small terminal segments of the labial palpi diverge laterally beyond the galeae and serve as sensory outposts. Back-and-forth movements of the tongue draw the food liquid into the canal of the proboscis, through which it ascends probably at first by capillary attraction, but before reaching the mouth the liquid is received into a preoral food channel on the base of the labium (fig. 9 A) between the bases of the maxillae, closed anteriorly by the epipharynx (B). Here at least the action of the sucking pump must become effective in finally drawing the liquid food into the mouth.

The proboscis as a whole is retractile and protractile by swinging back and forth on the long, suspensory rodlike cardines of the maxillae (figs. 3 A, 4 A, *Cd*), which are hinged to the sides of the cavity on the back of the head that lodges the bases of the maxillae and labium, but the tongue and the paraglossae themselves are deeply retractile into the end of the basal part of the labium (fig. 7 D, E).

The sucking pump of the aculeate Hymenoptera lies entirely within the head (fig. 10 A), and is clearly a combination of structures that in generalized insects constitute two distinct regions of the alimentary tract. The first is the true pumping apparatus (*Cb*); it is derived from the cibarial chamber of the preoral "mouth cavity," which primitively is a food pocket between the epipharyngeal wall of the clypeus and the base of the hypopharynx that is distensible by dilator muscles arising on the clypeus. The second part (*Phy*) represents the usual postoral pharyngeal dilatation of the stomodaeum. In the bee, as in most other sucking insects, the cibarial chamber has been enclosed within the head and converted into a sucking mechanism; but, while in Hemiptera and Diptera the pump is entirely a cibarial structure, in the Hymenoptera and Lepidoptera the cibarium and the pharynx are united to form a single pumping organ, in which, however, the cibarial and pharyngeal components may be identified. With the worker bee egestion is an important function of the feeding apparatus in the preparation of honey from nectar and in the feeding of the brood, the queen, and the drones; it is probable, therefore, that the sucking pump is also the principal regurgitative organ.

The salivary ejection apparatus of the bee is merely the salivary pocket, or salivarium, between the base of the hypopharynx and the base of the labium, into which commonly opens the salivary duct. The salivarium is converted into a closed chamber by the union of the hypopharynx with the anterior wall of the labium, and its

hypopharyngeal and labial muscles become antagonistic dilators and compressors of the salivary chamber thus formed. The saliva presumably is conveyed around the base of the tongue within the para-

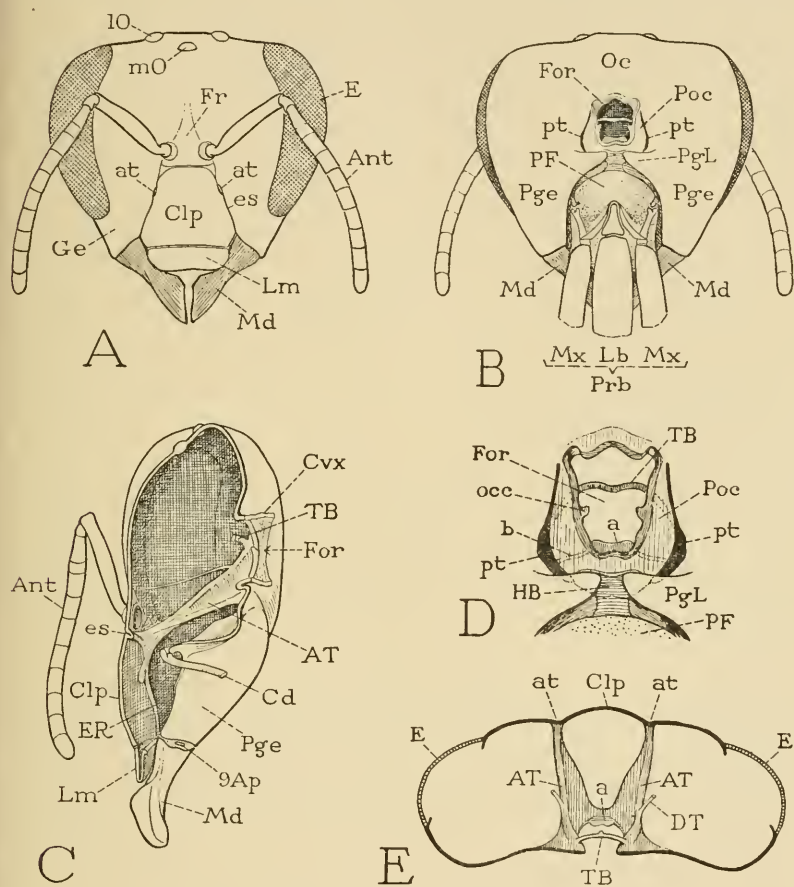


FIG. 1.—The head and cranial structures of the worker.

A, anterior view of head. B, posterior view of head, with bases of labium and maxillae. C, right half of head, mesal view, showing right tentorial bar. D, foramen magnum and associated structures, posterior view. E, horizontal section of head through upper part of foramen magnum and below bases of antennae, dorsal view.

*a*, shelflike plate on lower margin of foramen magnum; *b*, hollow bar from posterior tentorial pit (*pt*) to plate *a* on lower margin of foramen.

glossal lobes and carried out to the tip of the tongue through the salivary channel on the under side of the latter.

*The head.*—On the facial aspect of the bee's head (fig. 1 A) the significant feature is the unusual size of the clypeus (*Clp*), which

latter extends upward from the mandibles almost to the bases of the antennae beneath the strongly arched *epistomal sulcus* (*es*). The expansion of the clypeus is directly correlated with the great number of muscle fibers attached on its inner surface, which constitute the dilator muscles of the internal sucking pump (fig. 10 A, C).

On the back of the head (fig. 1 B) the opening into the neck, the *foramen magnum* (*For*), occupies a central position, and below it is the deep excavation of the cranial wall known as the *fossa of the proboscis* (*PF*), having a membranous floor in which are implanted the bases of the maxillae (*Mx*) and the labium (*Lb*). To the inflected sides of the fossa are articulated the rodlike maxillary cardines (*C*, *Cd*). Between the foramen and the fossa the broad postgenal walls of the cranium are connected by a subforaminal bridge. The median part of the bridge clearly is of hypostomal derivation, but the hypostomal element (*D*, *HB*) is constricted between a pair of mesally directed postgenal lobes (*PgL*). In Vespidae the postgenal lobes themselves are united in a *postgenal bridge*, and the more primitive *hypostomal bridge* is reduced to an internal ridge connecting an exposed subforaminal remnant with the hypostomal margin of the fossa. Thus, as stated by Duncan (1939), the subforaminal bridge of *Vespula* "consists chiefly of postgenal structures, though it does include a hypostomal component." In *Apis*, on the other hand, the bridge is chiefly hypostomal, but includes postgenal intrusions.

At the sides of the foramen magnum are the long posterior tentorial pits (fig. 1 B, *D*, *pt*), from which there extends forward and downward in the head a pair of strong tentorial bars (*C*, *E*, *AT*) attached anteriorly on the ridge of the epistomal sulcus (*C*, *ER*), with their roots marked externally by a pair of pits in the groove (*A*, *E*, *at*). These bars, except for their extreme posterior ends, represent the anterior arms of the tentorium as this structure is developed in more generalized insects. Just within the foramen magnum the longitudinal tentorial bars are connected dorsally by a narrow, arched rod, or *tentorial bridge* (*D*, *E*, *TB*), and shortly before the bridge each bar gives off a slender threadlike branch representing the usual *dorsal tentorial arm* (*C*, *E*), which extends forward but disappears before reaching the facial wall of the head. The tentorium of the bee, besides bracing the cranial walls, gives attachment to muscles of the antennae, the maxillae, the labium, the pharynx, and the oral plate of the sucking apparatus. From the deeper part of each posterior tentorial pit there extends into the head cavity a slender hollow rod (*D*, *b*), which is attached mesally

to a small plate (*a*) inflected from the lower lip of the foramen magnum.

*The antennae.*—The antennae arise close together near the center of the face (fig. 1 A, *Ant*), where each appendage is implanted in a small membranous area with a slightly elevated rim, known as the *antennal socket*. Each antenna (fig. 2 A, G) is divided by an elbow into two major parts, a basal stalk, or *scape* (A, *Scp*), and a long distal arm subdivided into 11 small sections in the female (A) and

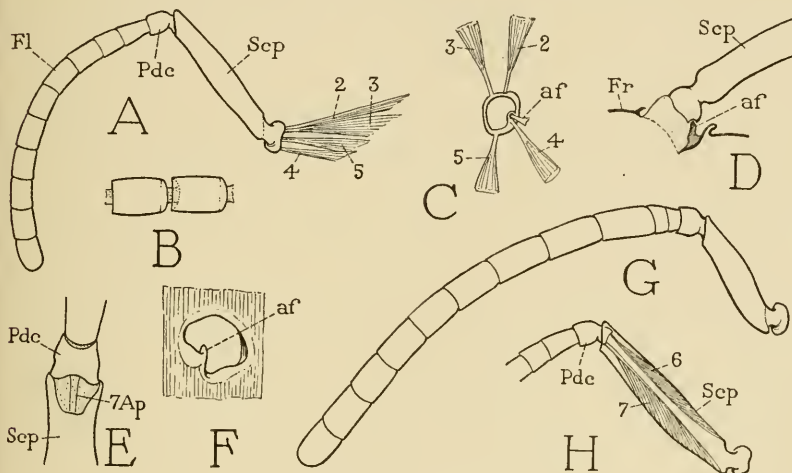


FIG. 2.—The antenna.

A, right antenna of worker and cranial muscles inserted on base, mesal view. B, two consecutive subsegments of flagellum pulled apart to show necklike membranous connection. C, inner rim of base of right antenna, showing position of muscle insertions. D, base of right antenna and section of antennal "socket" through antennal foramen (*af*), posterior view. E, joint between scape and pedicel, ventral view. F, rim of right antennal socket, anterior view. G, antenna of drone. H, proximal part of antenna of worker, showing muscles in scape inserted on pedicel.

12 in the male (G). The proximal piece of the arm is usually distinguished as the *pedicel* (*Pdc*), and the rest termed the *flagellum* (*Fl*), but in the bee there is no pronounced differentiation between these two parts. The flagellar subdivisions are not true segments since they are not articulated upon each other nor provided with muscles; the rounded base of each (B) fits into a distal depression of the one proximal to it, and the two are connected by a narrow, cylindrical, necklike membrane. The joint between the pedicel and the scape, on the other hand, has a dicondylic leglike articulation (E), and hence forms a definite transverse axis of movement, on which the pedicel and flagellum are turned up or down by levator and

depression muscles arising respectively on the dorsal and the ventral wall of the scape (H, 6, 7).

The scape of the antenna is articulated to the head by a distinct basal knob (fig. 2 D), which is pivoted on a small articular process, the *antennafer* (*af*), arising ventrolaterally from the rim of the antennal socket (*F*). The antenna is thus freely movable in all directions except as it is limited by the socket membrane. To provide for its movement four muscles arising on the concave dorsal surface of the tentorial bar of the same side of the head are inserted on the base of the scape (*C*), two above the level of the pivot and two below it.

*The labrum.*—The labrum of the honey bee (fig. 1 A, *Lm*) is a simple, transversely elongate flap with well-sclerotized, closely appressed outer and inner walls, and is freely suspended from the lower edge of the clypeus. It contains no compressor muscles (fig. 10 C, *Lm*), and is movable by only a single pair of extrinsic muscles arising on the frontal area of the head between the antennal bases, which are adductors since they are inserted by long tendons attached laterally on the posterior margin of the base of the labrum. In the wasps the labrum is retracted beneath the clypeus and the clypeal margin forms the lower edge of the face (fig. 9 E).

*The epipharynx.*—In both the wasps and the bees the epipharynx (figs. 9 E, 10 C, *Ephy*) is a preoral outgrowth of the inner, or "epipharyngeal," surface of the clypeus—not of the labrum. The epipharynx of the honey bee is a large, soft structure with a prominent median keel and padlike lateral lobes (fig. 9 A, *Ephy*). It is retractile by a group of divergent muscle fibers arising on the lower part of the clypeus (fig. 10 C, 25). Just above and behind the base of the epipharynx is the wide, oval mouth opening (figs. 9 A, 10 C, *Mth*) that leads into the cavity of the sucking pump. The epipharynx is richly provided with sense organs, but mechanically it serves, together with the lacinial lobes of the maxillae, to close the food channel on the base of the proboscis (fig. 9 A, B).

*The mouth.*—The wide aperture behind the epipharynx that leads into the sucking pump (figs. 9 A, 10 A, *Mth*) is the mouth of the bee in a functional sense, but since the anterior part of the pump (fig. 10 A, *Cb*) represents the primitively preoral cibarium lying between the clypeus and the hypopharynx, the true mouth, in a morphological sense, is between the cibarial and pharyngeal sections of the pump. In the Hymenoptera, therefore, as in various other sucking insects, the functional mouth is a secondary constriction of the food meatus between the inner face of the clypeus and the



anterior wall of the hypopharynx (fig. 10 A, *Mth*). In some of the Hymenoptera the mouth is guarded by a pair of long, valvelike lips, the upper one being the epipharynx, the lower one a fold from the lower edge of the mouth. In the bee the suboral fold hangs like a bib from the lower lip of the mouth (fig. 9 A, *bib*).

*The mandibles.*—The mandibles of the honey bee differ in shape and relative size in the three castes (fig. 3 F, G, J). In the worker (F) each mandible is elongate, thick at the base, narrowed through the middle, and widened again distally in a flattened expansion. The inner face of the expanded part is somewhat concave and traversed obliquely by a channel (*d*) fringed on both sides with hairs, which is continuous with a groove (*e*) that runs upward to the orifice of the mandibular gland (*f*) at the base of the jaw. The mandible is suspended from the lower lateral angle of the cranium (fig. 1 A, C), and has the usual two points of articulation, one with the lower part of the clypeus (fig. 3 E, *c*), the other (*a'*) with the subgenal margin of the cranium. The hinge line of the jaw between the two articulations slopes downward from in front, so that when the mandible is adducted its apex turns not only mesally but also posteriorly.

Each mandible has only two muscles, an *abductor* and an *adductor*. The fibers of the abductor spread over the lower part of the side wall of the head behind the compound eye (fig. 3 I, 8) and converge upon a stalked apodeme arising in the articular membrane at the outer side of the mandibular base (E, 8*Ap*). The large adductor muscle (H, 9) has several groups of fibers, some of which arise behind the eye above the abductor fibers, others on the back of the head below the level of the foramen magnum, while a small group (9*a*), inserted on a long slender branch of the apodeme, takes its origin on the top of the head. The strongly stalked adductor apodeme arises from the articular membrane at the inner side of the base of the mandible (fig. 1 C, 9*Ap*), and is closely applied to the mesal wall of the mandibular gland (fig. 3 F).

The worker bee makes various specific uses of its mandibles, including the collecting and breaking of pollen grains for food, manipulation of wax in comb-building, supporting the base of the extended proboscis while feeding on liquids, and holding the flexed proboscis in place when the latter is folded behind the head (fig. 3 B). The provision of each mandible with but two muscles gives the jaws active movements of abduction and adduction only, but there is sufficient flexibility at the articulations to allow of some play of the mandibles on each other. When the mandibles are used to hold the base of the extended proboscis, the channels on the inner surfaces

of their expanded ends fit exactly on the midribs of the maxillary galeae and allow the latter to slide between them. When the proboscis is folded (fig. 3 B) the mandibles are crossed behind the labrum against the bases of the flexed galeae, and thus hold the proboscis snugly against the head.

Passively the mandibles, when partly opened, form a conduit for the discharge of nectar or honey and of brood food from the mouth. According to Park (1925), "the honey is forced out over the dorsal surface of the folded proboscis between the mandibles which are held well apart"; and in a personal communication Frank E. Todd of the United States Bureau of Entomology and Plant Quarantine says, "feeding of royal jelly, and of honey and pollen, to the larvae is done through the mandibles."

The mandible of the queen (fig. 3 J) is of about the same length as that of the worker (F), but is bilobed distally and much wider at the base; it has a concavity on the inner face of the apical lobe, but there is no groove leading up to the orifice of the mandibular gland. The posterior surface is clothed with more numerous and longer hairs than the worker mandible, but in both castes of the female the mandibular hairs are unbranched. The mandible of the drone (G) is relatively and absolutely smaller than that of either the worker or the queen; its distal part is narrow, provided with a small apical tooth, and has a mesal depression from which a faintly marked groove leads up to the base of the jaw. The hairs of the drone mandible are particularly long and numerous, and, in contrast to those of the female mandible, are nearly all of the plumose variety.

The mandibular gland of the worker (fig. 3 F, *MdGld*) and the queen is a large sack lying between the facial wall of the head and the apodeme of the adductor muscle of the mandible. The gland in the worker extends upward to the level of the antennal bases, and in the queen is even larger. In the drone the mandibular gland is but a small vesicle at the base of the jaw. The secretion of the mandibular glands of the bee is said to serve for softening wax, but corresponding glands in other insects presumably have a "salivary" function in connection with feeding.

*The maxillae.*—The two maxillae (fig. 3 A) lie at the sides of the median labium rather than before it. The long *stipital sclerites* (*St*) of the maxillary bases are implanted proximally in the membrane of the proboscis fossa on the back of the head, and are suspended from the hypostomal margins of the fossa by the slender *cardines* (*Cd*), which also are contained in the fossal membrane. The free distal part of each stipes bears a long, broad, tapering *galea* (*Ga*), a large,

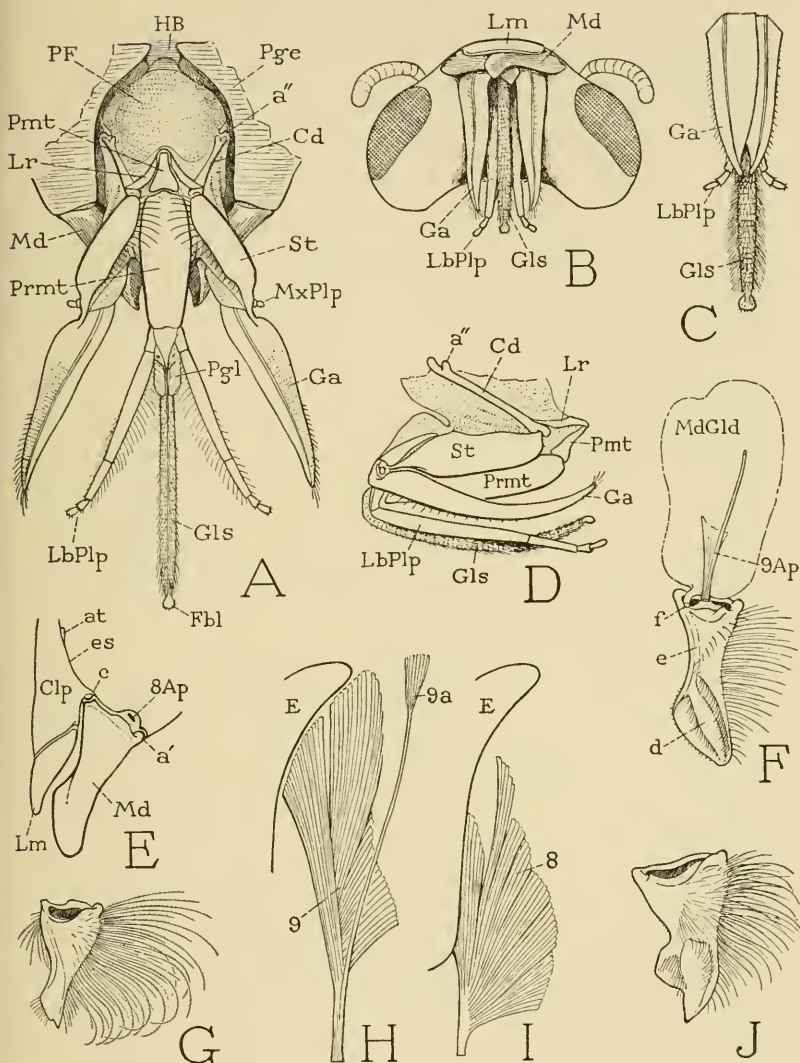


FIG. 3.—The mandibles, maxillae, and labium.

A, maxillae and labium of worker with parts artificially spread out behind the mandibles, suspended by maxillary cardines from margins of proboscis fossa (PF) on back of head. B, mandibles and free parts of maxillae and labium folded beneath head. C, distal parts of maxillae and labium assembled to form a proboscis, anterior view. D, lateral view of retracted and folded labium and left maxilla. E, left mandible of worker and adjoining parts of head, lateral view. F, right mandible of worker and mandibular gland, mesal view. G, right mandible of drone, mesal view. H, adductor muscle of right mandible of worker, arising behind compound eye. I, abductor of right mandible of worker. J, right mandible of queen, mesal view.

a', posterior articulation of mandible; a'', cranial articulation of maxillary cardo; c, anterior articulation of mandible; d, mesal depression of mandible; e, mesal groove of mandible; f, orifice of mandibular gland.

soft, cushionlike lobe arising mesad of the base of the galea, and a very small, 2-segmented, lateral *palpus* (*MxPlp*). A V-shaped sclerite, known as the *lorum* (*Lr*), which holds the basal plate of the labium in its apical angle, has its arms articulated with the distal ends of the maxillary cardines.

Each maxilla is provided with four extrinsic muscles arising within the head (fig. 4 A), one inserted on the cardo (*10*); the other three (*11*, *12*, *13*) on the stipes. The single cardinal muscle (*10*) is the usual promoter of the maxilla, which in generalized insects arises dorsally on the head wall and is inserted on the cardo anterior to the cranial articulation of the latter. In the bee, however, this muscle arises posteriorly on the postgenal inflection at the side of the proboscis fossa (fig. 1 C, *Pge*), and is inserted on a short lever arm of the cardo that projects above the articular condyle (fig. 4 A). By this shift in its point of origin the cardinal muscle becomes an effective protractor of the maxilla. The movement of the two maxillary cardines, however, affects both the maxillae and the labium because the three appendages are yoked at their bases by the V-shaped lorum (fig. 3 A, *Lr*). The muscles of the cardines in the bee, therefore, are *cardinal protractors of the proboscis*.

The long stipital muscles of the maxilla (fig. 4 A, *11*, *12*, *13*) are the primitive adductors, or functionally, protractors of a generalized maxillary appendage, that arise on the tentorium. In the bee these muscles have their origins on the extreme anterior ends of the longitudinal tentorial bars (*AT*), and hence at first sight appear to arise on the facial wall of the head. In most insects the stipital muscles act as protractors of the maxilla because their mesal pull (adduction) flattens the angulation between the cardo and the stipes and in this way protracts the appendage. The muscles evidently produce the same action in the bee, and become *stipital protractors of the proboscis*. Though the slant of the muscles in the fully protracted condition of the maxilla might suggest that the stipital muscles now become retractors, it is probable that the retraction of the proboscis is effected principally by the long cranial muscles of the labium (fig. 7 A, D, *17*).

The tapering bladelike galea of the maxilla is attached to the stipes by a prolongation of its base that forms a triangular plate, or *subgalea* (fig. 4 D, G, *Sga*), implanted laterally on the anterior surface of the distal end of the stipes. From the subgalea a strong midrib runs through the length of the galea to its tip. In the functional, protracted position of the proboscis the galeal blade extends straight out from



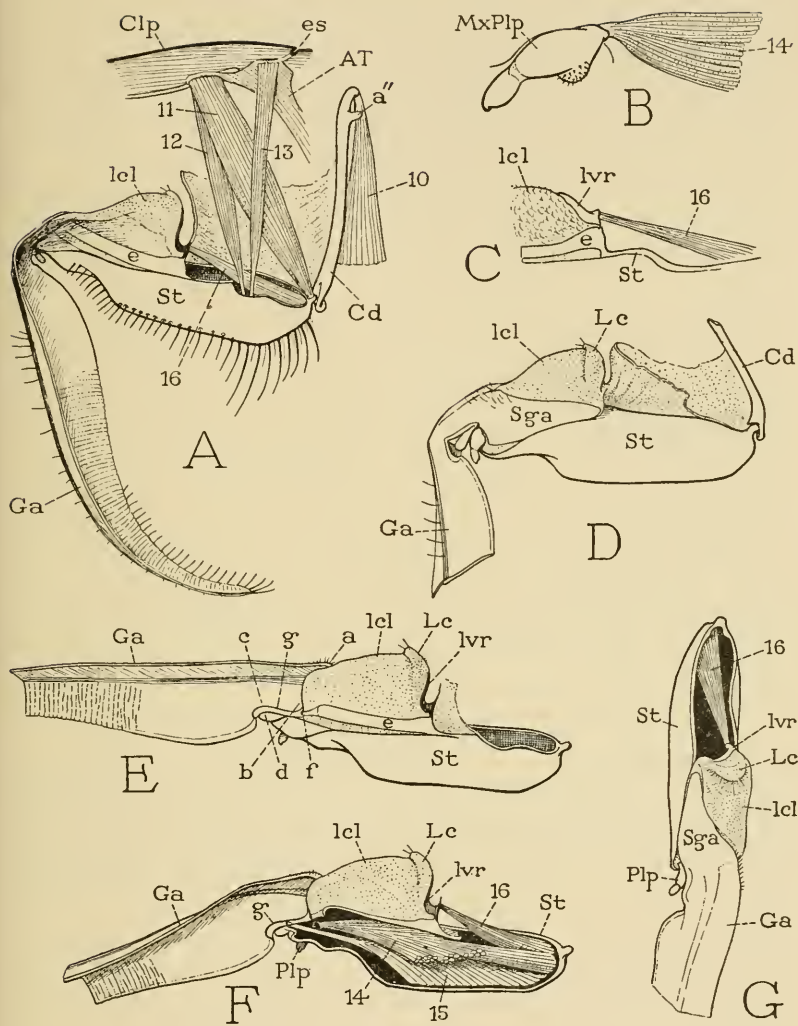


FIG. 4.—The maxilla.

A, right maxilla of worker and maxillary muscles, mesal view. B, left maxillary palpus and muscle, lateral view. C, lacinial lobe and lever of right maxilla of drone, mesal view. D, base of left maxilla of worker, lateral view. E, right maxilla with galea extended, mesal view. F, same, galea partly deflexed. G, stipes and base of galea of right maxilla, anterior view.

*a''*, cranial articulation of cardo; *a-b*, *c-d*, lines of flexure in base of galea; *e*, stipital arm in base of mesal wall of lacinial lobe; *f*, articular point of galea on *e*; *g*, leverlike marginal ridge on base of galea articulating with articular point (*f*) of stipes.



the stipes (fig. 4 E), its broad outer part being vertical and the narrower mesal part horizontal, as the two galeae overlap to form the roof and the sides of the temporary proboscis canal (figs. 3 C, 9 C). When the proboscis is retracted the galea is bent back and folded upside down below or behind the stipes (fig. 3 D).

The folding of the galea is produced by a single muscle arising in the stipes (fig. 4 F, 15), which evidently represents the usual galeal flexor of other insects. The action of the muscle in the bee, however, depends on a special device in the base of the galea. Where the galea joins the subgalea it is abruptly narrowed, and the lateral margin of the narrow part is thickened to form a small leverlike ridge (E, *g*) that articulates proximally on the tapering, laterally curved end (*f*) of a long narrow sclerite (*e*) in the mesal wall of the stipes. On the middle of the lever ridge is attached the tendon of the flexor muscle of the galea (F, 15). The tension of the muscle in contraction first depresses the galea and turns it backward and outward because of the obliquity of the line of bending (E, *a-b*) between the galea and the subgalea; but a second line of bending (*c-d*) beyond the first and oblique in the opposite direction soon counteracts the lateral movement, so that the continuing pull of the muscle finally turns the galea straight back and folds it up against the stipes. The extension of the galea evidently results automatically from the elasticity of its base and its basal continuity with the firmly affixed subgalea (G).

The large, soft, cushionlike lobe of the stipes that arises at the mesal side of the subgalea (fig. 4 A, D, F, G, *lcl*) is a prominent feature of the bee's maxilla. On its proximal end is a small subsidiary lobe (D, G, *Lc*) bearing a few small setae, which, by comparison with other Hymenoptera (fig. 5), evidently represents the maxillary *lacinia*. In a vespoid wasp (fig. 5 A, B) the lacinia is a well-developed lobe (*Lc*) arising from the stipes mesad of the base of the larger galea (*Ga*). In *Bombus* (D) and *Xylocopa* (E) the lacinia is a small setigerous or spiny lobe overlapping a large membranous area of the stipes. It would appear, therefore, that the major part of the large cushionlike lobe of the maxilla in *Apis* (fig. 4 D, *lcl*) is a development of the sublacinial membranous area present in *Bombus* and *Xylocopa*, and that the small setigerous lobule (*Lc*) on its base is a remnant of the lacinia proper. The entire structure in *Apis* is here termed the *lacinial lobe*; it plays an important part in the closure of the food channel on the base of the proboscis.

In the steeply declivous proximal wall of the lacinial lobe is a small curved sclerite (fig. 4 E, *lvr*) with a tapering distal arm and a thickened base, which latter is connected by a fulcral point with the

proximal end of the narrow mesal sclerite (*e*) of the stipes. The lacinial sclerite serves in the bee as a lever for keeping the lobe erect. On the upper point of its base is inserted a muscle from the stipes (F, 16), the contraction of which revolves the lever on its fulcrum and thus exerts a tension on the lobe. The lacinial lobe is the "Segelhalter" of Wolff (1875), who notes the lever sclerite in its base, and terms its muscle the "Spanner des Segelhalters." The muscle represents the flexor of the lacinia in generalized insects; the lever apparatus is present also in other Hymenoptera. In *Vespula* (fig. 5 A,

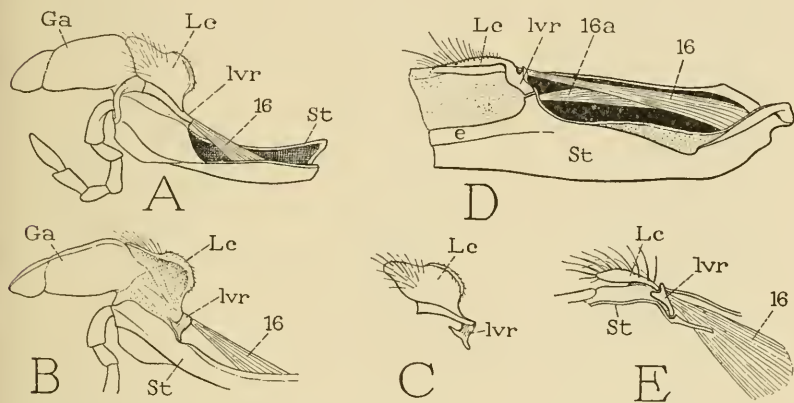


FIG. 5.—Examples of the maxillary lacinia in Vespidae and Apoidea.

A, left maxilla of *Vespula maculata* (L.), with well-developed lacinia, dorso-lateral view. B, right maxilla of same, ventromesal view. C, detached lacinia of left maxilla of same, lateral view, showing mesal lever arm (*lvr*). D, base of right maxilla of *Bombus americanorum* (F.), with small lacinia attached to large membranous area, mesal view. E, right lacinia and lever sclerite of *Xylocopa virginica* (L.), mesal view.

B, C) a small sclerite (*lvr*) in the base of the lacinia, giving insertion to the lacinial muscle (A, B, 16), curves around the proximal end of the lacinia to articulate on the stipes (B). In *Bombus* (D) the base of the lacinia itself articulates with the stipes, but in *Xylocopa* (E) there is a distinct lever sclerite (*lvr*) giving insertion to the lacinial muscle (16).

The minute, two-segmented palpus of the maxilla (fig. 3 A, *MxPlp*) arises from the end of the stipes laterad of the base of the galea, and is provided with a large muscle (fig. 4 B) arising in the stipes (F, 14). It is not evident why so small and seemingly unimportant an organ should have a muscle of such size. Wolff (1875) believed that the palpus muscle serves as an extensor of the galea, and Morison (1927) regarded it as a muscle of the galea, which, he says

mistakenly, is attached "near" the base of the palpus. There can be no question that the muscle is inserted directly on the base of the palpus (fig. 4 B), and it is not clear how it could act as an extensor of the galea. Duncan (1939) says there are two muscles for each maxillary palpus in *Vespula* inserted on the palpal base.

*The labium and hypopharynx.*—The labium of the bee presents externally all the parts of a generalized labial appendage (fig. 3 A). The lengthened base contains a small, triangular *postmental sclerite* (*Pmt*) and a long trough-shaped *premental plate* (*Print*). Diverging from the end of the prementum are the slender, four-segmented *labial palpi* (*LbPlp*), each supported on a small basal stalk, and between the latter arise the ligular lobes, including the long, median, so-called *tongue* (*Gls*), which is probably the combined glossae, and a pair of short lateral *paraglossae* (*Pgl*). The postmentum and the proximal part of the prementum are suspended in the membranous floor of the fossa of the proboscis (*PF*) on the back of the head, and are membranously united also with the bases of the maxillary stipites. The apex of the postmentum is embraced by the angle of the lorum (*Lr*), and turns in the latter when the proboscis is protracted or retracted. In the completely retracted position the apex of the lorum rests in the depression of the hypostomal bridge (*HB*).

The premental sclerite covers only the posterior and lateral walls of the premental area of the labium, the anterior wall being entirely membranous (fig. 6 A, 7 D). The membranous anterior wall ends in a transverse inflection at the bases of the ligular lobes (fig. 6 A), and in this groove, as may be seen by separating the paraglossae (B), is the opening of the salivary ejection apparatus (*SIO*). The apparent anterior wall of the prementum, therefore, represents the *hypopharynx* (B, *Hphy*) adnate upon the labium, since the salivary duct in generalized insects opens between the hypopharynx and the labium. The hypopharyngeal surface in the bee, furthermore, extends up to the functional mouth (fig. 10 A, *Hphy*), and includes the oral plate (*opl*) on the floor of the mouth cavity at the entrance to the sucking pump and the biblike fold (*bib*) that hangs down from the margin of the plate. The ascendent hypopharyngeal surface is flanked by a pair of slender *suspensorial rods* (figs. 7 D, 9 A, *s*) that extend from the base of the prementum to the mouth angles, and probably represent lateral hypopharyngeal sclerites of generalized insects.

The ligular lobes of the labium have a common base which is continuous with the prementum (fig. 6 A, B, C), but is supported on the latter anteriorly by a pair of *ligular arms* (A, B, *h*), and posteriorly by a triangular *subligular plate* (C, *k*). The ligular arms are sclerotic bands arising from the anterior margins of the premental plate; at

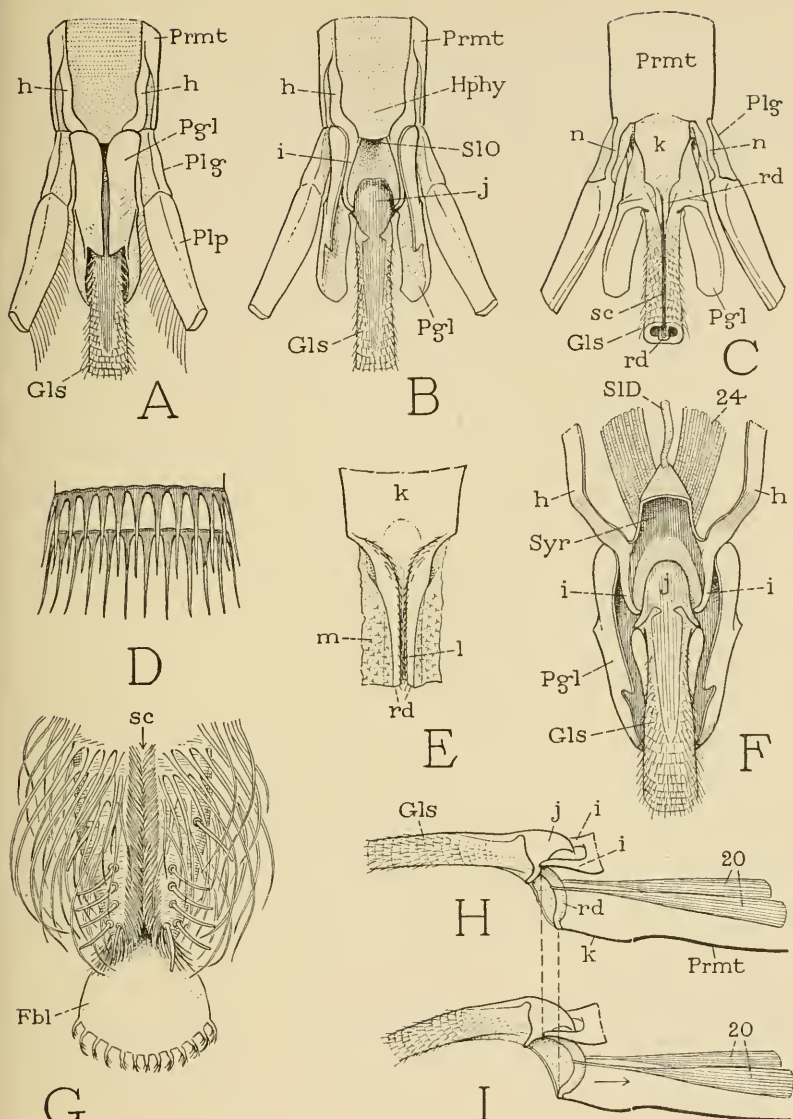


FIG. 6.—The labium of the worker.

A, end of prementum with ligula and bases of labial palpi, anterior view, paraglossae in natural position. B, same, paraglossae spread apart exposing salivary opening (SIO). C, same, posterior view, showing base of glossal rod (rd) and entrance to salivary channel (sc). D, two tiers of glossal hairs, anterior view. E, base of glossal rod exposed by eversion of salivary channel. F, ligula and salivary syringe, anterior view, anterior wall of syringe removed. G, end of glossal tongue, posterior view. H, diagram of base of protracted tongue. I, same, tongue partly retracted by contraction of glossal muscles (20). *h*, ligular arm of prementum; *i*, pivotal process of base of tongue; *j*, basal plate of tongue; *k*, subligular plate of prementum; *l*, canal of glossal rod; *m*, membranous wall of salivary channel; *n*, elastic posterior rod of labial palpiger; *rd*, glossal rod; *sc*, salivary canal of tongue.



the base of the ligula they are inflected laterad of the salivary opening (B), and are then continued as a pair of slender processes (*i*) that support the bases of the paraglossae laterally, and finally curve inward to form a pair of fulcral points articulating with the base of the tongue (*j*). The subligular plate (C, *k*) is directly continuous from the prementum, but is flexible on the latter, and its apex is produced into the rod (*rd*) that traverses the channel of the tongue.

The long, cylindrical, densely hairy glossal tongue of the honey bee has a closely ringed structure, in which hard circles bearing the hairs alternate with membranous smooth areas (fig. 6 D), so that the organ is both flexible and contractile. The posterior, or under, surface presents a narrow median groove (C, *sc*) that expands within the tongue into a wide thin-walled channel. The inner wall of the channel is traversed by a slender, elastic rod (*rd*), which is itself grooved on its outer surface (E), and the groove is fringed with small hairs directed distally. The lips of the glossal channel spread apart at the base of the tongue (C) and expose the proximal end of the rod, which is here seen to be directly continuous with the apex of the subligular plate (C, E, *k*). Distally the rod ends in a small, freely projecting, spoon-shaped terminal lobe of the tongue, known as the *flabellum* (G, *Fbl*). The convex under surface of the flabellum is smooth, but the distal margin and the upper surface are covered with small branched hairs. The base of the tongue is somewhat thickened; anteriorly it is covered by a hard, bonnet-shaped sclerite (F, H, *j*) decurved abruptly before the salivary orifice and produced distally in a tapering plate on the tongue surface. The basal sclerite is embraced laterally by the fulcral processes (*i*) of the ligular arms of the prementum, which hold the tongue firmly in place, but allow it to revolve freely in a vertical plane on the transverse axis between their opposing points.

The paraglossae are thin, elongate lobes arising from the common ligular base at the sides of the tongue (fig. 6 A, B, C, *Pgl*), where they are attached to the sides of the distal process of the ligular arms (B, *i*) that form the fulcral points of the tongue. The concave mesal surfaces of the paraglossae clasp the base of the tongue (A) and underlap its posterior surface, thus covering the proximal end of the tongue channel. The paraglossae automatically assume this position; they are not individually movable, since no muscles are attached directly on them.

The salivary ejection apparatus, which may be termed the *salivary syringe*, opens by a wide aperture situated, as already noted, anteriorly at the distal end of the prementum just behind the declivous base of



the tongue (fig. 6 B, *SIO*). The aperture leads into a wide, flat, triangular chamber (F, *Syr*, exposed here by removal of a part of the anterior wall), into the inner end of which opens the salivary duct (*SID*). The floor of the chamber is a rigid, slightly concave plate continuous at its distal angles with the inflected ends of the ligular arms of the prementum (*h*), which flank the salivary orifice (B). The roof is flexible and elastic, and gives insertion to a pair of convergent dilator muscles (fig. 7 A, 23) arising on the anterior edges of the premental sclerite. A pair of much larger muscles arising in the base of the prementum (figs. 6 F, 7 A, C, 24) and inserted on the lateral margins of the syringe evidently act as expulsors of the saliva by flattening the dilated chamber. The salivary muscles are effective only in the protracted condition of the proboscis; as they are shown in figure 7 A the muscles are slack and nonfunctional because of the retraction of the ligula into the prementum.

The salivary syringe of the bee is an elaboration of the usual salivarium, which in generalized insects is a mere pocket between the hypopharynx and the base of the labium. The union of the hypopharynx with the labium has converted the salivary pocket into a closed chamber, and the ordinary hypopharyngeal and labial muscles of the salivarium become, respectively, dilators and compressors of the syringe.

The saliva, forcibly expelled from the salivary syringe, encounters at once the steeply declivous base of the tongue, which lies immediately before the salivary orifice (fig. 6 B). It must, therefore, be deflected in two divergent streams past the sides of the tongue into the concavities of the mesal surfaces of the paraglossae, and by the latter conveyed to the posterior surface of the tongue. Here, presumably, the saliva enters the tongue channel and runs through it to the tip of the organ, where it flows out on the under surface of the apical flabellum (fig. 6 G). It must be admitted that, so far as known to the writer, no direct observations have been made on the course of the saliva in a living bee; the relations of the structural parts concerned, however, would seem to leave no other course available than that described above, except, perhaps, that the actual conduit of the saliva through the tongue may be the groove of the glossal rod instead of the larger channel that opens on the surface of the tongue. The hair-fringed groove of the rod clearly must have some specific function.

It is possible that the same apparatus may be used also in the process of "ripening" nectar into honey, during which process, as described by Park (1925), nectar extruded from the mouth is said to

flow over the upper surface of the proboscis and to swell into a globule in the posterior angle of the proboscis between the recurved free distal parts and the basal parts of the latter. The nectar globule is several times sucked back into the mouth and redischarged. Though recorded observations are not specific as to the exact course of the nectar around the base of the tongue, it is much to be suspected that the passageways between the tongue and the paraglossae, and likewise the glossal channel itself, the wall of which is eversible, serve to conduct the nectar in both directions.

The principal movements of the labium are (1) the back-and-forth motion of the labium with the maxillae when the entire proboscis is retracted and protracted, (2) an independent movement of the labium between the maxillae, (3) individual movements of the tongue during feeding, and (4) the backward flexion of the tongue and palpi when the proboscis is not in use. The flexion of the tongue accompanies the retraction of the proboscis, and involves a retraction of the base of the ligula into the end of the prementum. Other minor movements, probably depending on muscle tension, adjust the various parts to their functional positions.

The extrinsic musculature of the bee's labium consists of two pairs of muscles corresponding with the anterior and the posterior labial adductors of generalized insects inserted on the prementum. The anterior labial muscles in the bee (fig. 7 D, 17) are the longest muscles of the head; they arise on the dorsal wall of the cranium, go downward through the head, traverse the prementum (A), and insert by tendons on the distal ends of the ligular arms (A, D, h) of the prementum. These muscles are *labial retractors of the proboscis*, since their contraction affects not only the labium but the maxillae as well. Also they take part in the retraction of the ligula into the end of the prementum (A, E), which causes the deflexion of the tongue. The posterior labial muscles (D, 18) arise on the anterior ends of the tentorial bars of the head and converge posteriorly to a single median tendon attached on the proximal extremity of the prementum. These muscles probably act as protractors of the labium by flattening the angle between the postmentum and prementum, thus giving the labium an independent movement between the maxillae, and in addition they draw the prementum toward the mouth during feeding. The posterior labial muscles may, therefore, be termed *protractor-adductors of the labium*.

The movements of the tongue during feeding, or when the bee is exploring a food source, consist of lengthwise extensions and contractions of the organ, and lateral movements of the part projected

beyond the galeae and palpi. The movements are so varied and rapid that the tongue itself seems to be endowed with mobility. Only two muscles, however, account for the activity of the tongue, and they are inserted on the base of the axial rod. These muscles (fig.

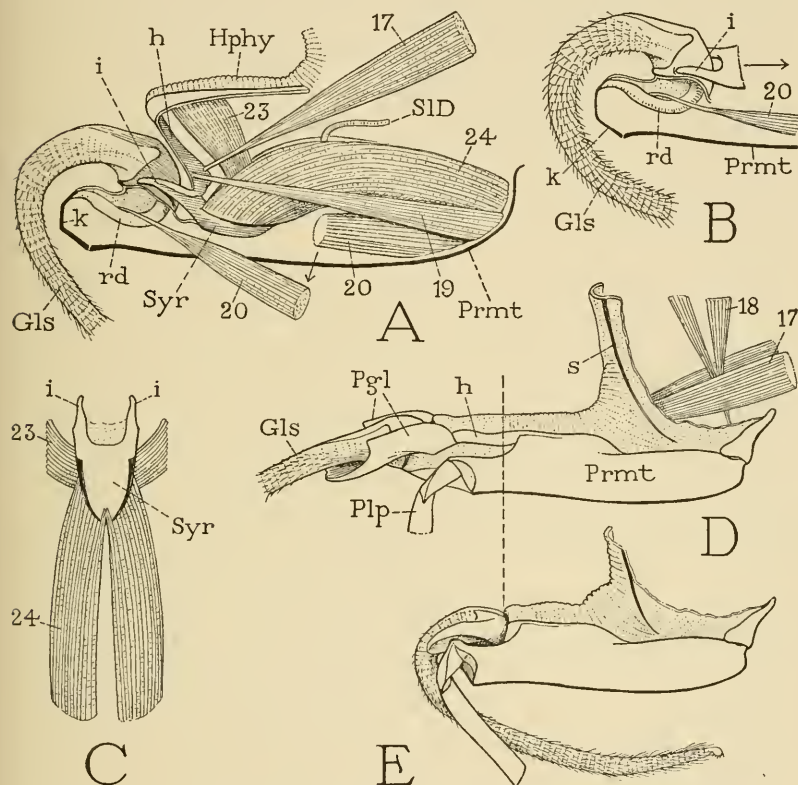


FIG. 7.—The mechanism of ligular retraction, and the salivary syringe.

A, lengthwise section of prementum of worker with ligula and salivary syringe retracted by pull of muscles 17 and 19 on ends of ligular arms (*h*), salivary muscles inoperative. B, detail of base of retracted tongue. C, salivary syringe and muscles, posterior view. D, prementum, with ligula protracted. E, same, ligula retracted as at A.

*h*, ligular arm of prementum; *i*, pivotal process of *h* supporting base of tongue; *k*, subligular plate of prementum supporting base of glossal rod; *s*, suspensorial rod of hypopharynx.

6 H, 20), arising in the base of the prementum (fig. 7 A), undoubtedly represent the usual flexors of the two glossal lobes of generalized insects. The rod of the bee's tongue is continuous distally with the flabellum, it traverses the inner wall of the membranous glossal channel, proximally it turns backward (fig. 6 H, *rd*) and is

attached to the apex of the subligular plate (*k*) at the end of the prementum. The two muscles of the rod (*20*) are attached by tendons, not directly on the rod, but immediately at the sides of its recurved basal part. It is clear that the contraction of the muscles increases the basal curvature of the rod (*I*), and therefore pulls the rod back through the tongue as far as the membranous wall of the enclosing channel will permit. The tongue is thus shortened, owing to the compressibility of its ringed wall, particularly in its distal part. On relaxation of the muscles the tongue is again extended, evidently by the elasticity of the rod and the compressed tongue wall, since there is no specific extensor mechanism. Furthermore, the attachment of the muscles at the sides of the rod enables the muscles by acting singly and alternately to revolve the rod, and thus probably are effected the varied lateral movements of the tip of the tongue.

We may now examine the mechanism by which the base of the ligula is retracted into the end of the prementum and the tongue turned back behind the head in the position it assumes when the proboscis is retracted (fig. 3 B, D). In the functionally protracted condition of the labium (fig. 7 D) the tongue and the paraglossae are extended from the end of the prementum and their bases are fully exposed. In the retracted state (E) the base of the ligula is deeply sunken into the end of the prementum, and the tongue is sharply bent backward behind the latter. It is to be seen also that the ligular arms of the prementum (D, *h*) have been completely folded inward, and that the subligular plate is angularly bent upward (B, *k*). The position of the parts concealed by retraction is best seen in a sectional view (A).

The retraction of the ligula is brought about by two pairs of muscles inserted on the distal ends of the ligular arms of the prementum (fig. 7 A). One muscle of each pair is the long retractor of the labium (*17*) arising in the top of the head; the other muscle (*19*) arises in the base of the prementum, and probably represents the paraglossal muscle of other insects. The pull of these muscles on the ends of the ligular supports (*h*) inflects the latter into the membranous distal end of the prementum, and consequently retracts the attached tongue, paraglossae, and salivary syringe, while the subligular plate (*k*) is bent forward and upward beneath the base of the tongue.

The base of the retracted tongue (fig. 7 A, B), held by the pivotal processes (*i*) of the ligular arms, is separated by a considerable distance from the end of the subligular plate (*k*), to which the tongue rod (*rd*) is affixed. As a consequence the rod has been drawn in a wide loop far out of the base of the tongue. Since the rod traverses



the posterior part of the tongue in the ample membrane of the glossal channel, the contractile and flexible tongue is not only shortened by the retraction of the rod, but is sharply curved in a posterior direction. Thus the retraction of the proboscis by the retractor muscles of the labium effects also the retraction of the base of the ligula into the prementum, and the latter action produces automatically the shortening and posterior flexion of the tongue. The salivary syringe also is pulled inward by the inflection of the ligular arms, and in the retracted condition its muscles are slack and temporarily functionless. Inasmuch as there is no muscular mechanism for the protraction of the ligula, it must be assumed that the parts are extended by the elasticity of the inflected ligular arms and the subligular plate when the retractor muscles relax.

The long, 4-segmented labial palpi (fig. 8 A) arise from the distal end of the prementum, where each palpus is supported on a small basal lobe (*Plg*) commonly regarded as being a palpiger, i.e., a palp-supporting lobe of the prementum, rather than a basal segment of the palpus. In nonconformity with this idea, however, the single muscle of the palpus (*21*) is attached within the basal lobe. The palpus itself contains only one muscle (*22*), which arises in the long first segment and is attached mesally on the base of the succeeding segment; it flexes the distal part of the palpus, which, when released, springs back to the extended position by its own elasticity.

The flexing mechanism of the entire palpus, by which the palpus is turned back behind the prementum when the proboscis is retracted, is in the small palpiger. Each palpiger is flattened from side to side, and its walls are membranous except for a narrow sclerotic bridge in the anterior wall, which connects the first palpus segment with the prementum (fig. 8 A), and a slender, flexible and elastic rod in the posterior wall (A, D, *n*) that is continuous from the prementum to the midrib of the palpus. The basal muscle of the palpus (B, *21*) is attached by a long tendon on the posterior rod a little beyond the middle of the latter. When the palpus is extended (B) the rod is slightly curved into the rear wall of the palpiger; when artificially flexed (C) the palpus is turned back with its lateral surface posterior, and the elastic rod of the palpiger (*n*) is strongly curved into the posterior wall of the palpiger. There can be little question, therefore, that the flexing of the palpus results, conversely, from an incurving of the rod by the pull of the muscle attached on it, and, in fact, the action can be demonstrated in a dead bee by pressing the rod so as to bend it into the palpiger. The exact movements of the palpus.



however, depend on the obliquity of lines of bending at the ends of the palpiger (B, *a-c*, *b-c*, and *b-d*).

The movements of the palpiger can be well illustrated with a piece of stiff paper cut into the form shown at E of figure 8 and creased

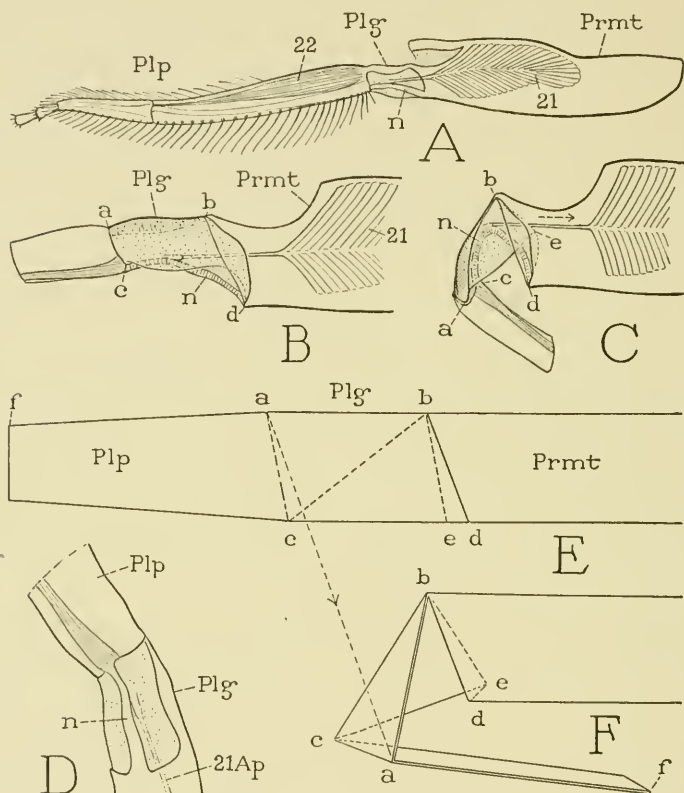


FIG. 8.—The labial palpus.

A, right palpus, palpiger, and prementum, mesal view, showing muscles. B, base of palpus in position of extension from prementum. C, same, palpus flexed. D, base of palpus, posterior view, showing elastic rod (*n*) in posterior wall of palpiger, and attachment of flexor muscle tendon. E, F, diagrams of flexing of palpus on prementum, illustrated with piece of paper cut and creased as at E, and folded as at F.

*a-c*, *b-d*, lines of folding at ends of palpiger; *b-c*, line of diagonal folding of palpiger; *b-e*, line of infolding at base of flexed palpiger; *f*, distal point on palpus; *n*, elastic rod in posterior wall of palpiger.

along the lines *a-c*, *b-c*, *b-d*, and *b-e*. By folding outward along the diagonal (*b-c*) through the "palpiger" the triangle *abc* is turned over and directed downward (F); the "palpus" can now be bent backward in a horizontal position, but its alignment with the "prementum" necessitates a compensating fold inward along the lines *b-d* and *b-e*.

The distance from *c* to *d* is thus shortened, and, by reversing the sequence of the movements, the approximation of *c* and *d* would produce the folding. In the palpiger of the bee (B) this shortening results from the inward curvature of the rod (*n*) effected by the pull of the muscle on its convex side, and the palpus automatically turns over and bends backward (C). Extension of the flexed palpus evidently depends on the elasticity of the palpiger, since there is no extensor muscle.

*The preoral food channel.*—The membranous anterior, or hypopharyngeal, wall of the labium extends upward from the salivary orifice at the distal end of the prementum to the mouth, and forms the floor of a deep *preoral food channel* between the maxillary bases (fig. 9 A, *FC*) that is continuous with the closed food canal of the distal part of the proboscis (C, *fc*). The wide aperture of the mouth (A, *Mth*) at the upper end of the channel lies behind the base of the epipharynx (*Ephy*), and the epipharynx is covered by the projecting labrum. On the floor of the mouth is the broad *oral plate* (fig. 10 A, B, *opl*), from which depends the large, thin, double-pointed, triangular fold (*bib*) that hangs like a bib from the lower lip of the mouth over the adoral hypopharyngeal surface (fig. 9 A, *bib*). At the sides of the bib in the hypopharyngeal membrane are the slender hypopharyngeal suspensory bars (*s*), which taper downward to the sides of the prementum.

When the proboscis is depressed or retracted, the mandibles are able to close before the mouth between the labrum and the bases of the maxillae. If the mandibles are spread apart when the proboscis is protruded the preoral food canal is widely exposed (fig. 9 A) and the lacinial lobes of the maxillae (*lcl*) are prominently displayed on the mesal margins of the stipites. When the proboscis is fully extended in the functional position, the mandibles are opened, allowing the base of the proboscis to swing up between them, and they now clasp the bases of the galeae. In this position, the proboscis extends straight out from before the mouth; the formerly vertical floor of the preoral food channel becomes more nearly horizontal, and the cushion-like lacinial lobes of the maxillae are pressed into the lateral concavities of the epipharynx, with the median keel of the latter closing the space between them (fig. 9 B), while the labrum clamps down on the epipharynx. The preoral food channel on the base of the proboscis is thus converted into a closed passageway, by which the food canal of the distal part of the proboscis is put into communication with the mouth. The approximation of the labium to the mouth bows the suspensorial rods (A, *s*) outward and accentuates the

depression between them into a deep heart-shaped cavity. The bib dependent from the lower lip of the mouth, however, has now assumed a nearly horizontal position with its points resting on the hypopharyngeal surface of the prementum, and thus forms a ramp from the floor of the food channel to the mouth, bridging the cavity behind it.

The cavity temporarily formed behind the suboral fold in the bee by the infolding of the adoral hypopharyngeal surface (fig. 10 A, C, *IbS*) evidently corresponds with the permanently differentiated *infrabuccal sac* of certain other Hymenoptera. In Vespidae the sac is a well-developed structural feature of the preoral cavity, completely closed except for a narrow, transverse slitlike opening (fig. 9 D, *IbS*) beneath a broad suboral fold (*bib*) corresponding with the bib of the honey bee.

The preoral feeding mechanism of the wasps, as described by Duncan (1939) in *Vespula*, is similar to that of the bee, except for the more highly developed infrabuccal sac. The hypopharyngeal rods are shorter and thicker in *Vespula* (fig. 9 D, E, *s*) than in *Apis*, and are termed by Duncan the "labral tractors" because when the proboscis is extended they pull down on the long basal angles of the labrum (E, *Lm*) and thus open the mouth. The labrum of the wasp, however, is entirely detached from the edge of the clypeus (*Clp*) and is retracted beneath the latter. The epipharynx of the wasp, according to Duncan, has no muscles; in the bee it is provided with a group of muscle fibers arising on the clypeus (fig. 10 C, *25*). A short branch of each hypopharyngeal rod in *Vespula* (fig. 9 D, E, *x*), the "tractor suspensor" of Duncan, goes laterally to the base of the mandible, and is suggestive of being the mandibular arm of the lateral hypopharyngeal sclerite of generalized insects, on which the hypopharyngeal muscle of the mandible, when present, is attached.

Just within the mouth on the floor, or posterior wall, of the entrance to the sucking pump is the broad oral plate (fig. 10 A, *opl*), which is commonly known as the "pharyngeal plate." There can be little doubt, however, that the plate in question is a hypopharyngeal structure, since from its proximal angles two long arms (A, B, C, *y*) extend upward and anteriorly in the lateral walls of the pump and give attachment to muscles arising on the frons (B, C, *32*, *33*). Similar though shorter rods giving insertion to frontal muscles are present in most insects, and usually are prolongations from hypopharyngeal sclerites; the rods, together with their muscles, in fact, constitute the adductor apparatus of the hypopharynx. In some cases the pharyngeal rods are processes of a plate on the base of the

hypopharynx, but the structure as developed in the bee (B) is characteristic of the Hymenoptera.

In the honey bee the food glands that furnish the so-called royal jelly open by pores on the distal angles of the oral plate (fig. 10 B, o). It may be noted incidentally, therefore, that these glands are *hypopharyngeal glands* and not "pharyngeal" glands as they are generally

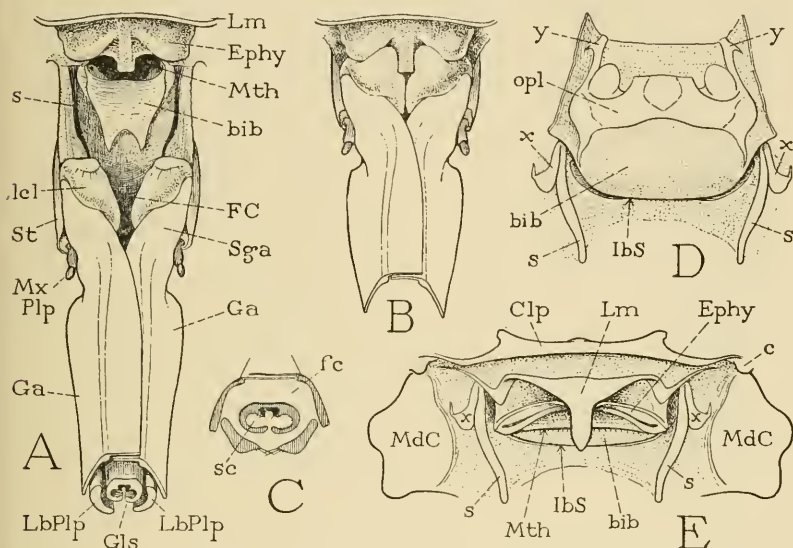


FIG. 9.—The preoral food channel and the mouth region in *Apis* and *Vespa*.

A, base of protracted proboscis of worker bee, anterior view, exposing the epipharynx, mouth, bib, and food channel between lacinial lobes of maxillae. B, same, base of proboscis retracted, food channel closed by lacinial lobes pressed against epipharynx. C, cross section through distal part of proboscis. D, mouth region of *Vespa maculata* (L.), anterior wall of sucking pump removed, showing oral plate (opl), suboral bib (bib), and closed entrance to infrabuccal sac (IbS). E, same in natural condition, ventral view, mouth closed to a narrow slit (Mth) above closed entrance to infrabuccal sac (IbS), overhung by labrum (Lm).

c, anterior articulation of mandible; s, suspensorial rod of hypopharynx; x, mandibular branch of s; y, pharyngeal arm of oral plate.

termed. Their secretion discharged upon the hypopharyngeal bib evidently accumulates in the food channel on the base of the proboscis, where it becomes accessible to other adult bees. The open food channel thus serves as a feeding trough for the queen and the drones when the latter are being fed by the workers. The muscles attached on the pharyngeal arms of the oral plate would appear to give movements to the oral plate and the bib that might facilitate the expulsion of the royal jelly into the feeding trough, but the plate with its arms



and their muscles is present in the drones and the queen of the honey bee, and also in other Hymenoptera that do not have food glands.

*The sucking pump.*—The organ by which the bee draws liquids through the closed canal of the proboscis and into the mouth and passes them on to the oesophagus is a large sack with strongly muscular walls lying in the head. This sack, the *sucking pump* (fig. 10 C), extends from the mouth upward and posteriorly (A) to the level of the foramen magnum, where its narrowed upper end rests on the tentorial bridge (TB) and passes into the slender oesophagus (Oe), which goes posteriorly through the foramen.

The sacklike sucking pump (fig. 10 A, C), though its outlines are continuous, is differentiated by structural features into two parts, a larger upper part (A, *Phy*) ensheathed in circular muscle fibers, and a smaller lower part (Cb) with a strong musculature of dilator and compressor fibers on its anterior wall (C). The upper part unquestionably is the pharynx: the frontal ganglion (A, *FrGng*) lies against the lower part of its anterior wall, the arms of the oral plate (y) traverse its lateral walls, its dilator muscles (*dlphy*) arise on the frontal region of the cranium and are inserted *above* the frontal-ganglion connectives—all of which characters, together with the ensheathment by circular muscle fibers, are diagnostic of the pharynx. The lower part of the organ (A, Cb) has five pairs of large bundles of dilator muscle fibers attached on its anterior wall (C, 26-30), and these muscles arise on the clypeus. This part of the pump, therefore, must be derived from the cibarium of generalized insects, which is a pocket of the preoral cavity between the under surface of the clypeus and the base of the hypopharynx. The hypopharyngeal floor of the cibarial section of the pump in the bee is represented by the oral plate (*opl*). In addition to the dilator muscles the cibarium is provided with thick bands of compressor fibers (C, 31) running obliquely between the dilator bundles from the side of the oral plate to the median area of the anterior wall, where they turn dorsally. In addition a strong anteriormost group of compressor fibers arches over the mouth. In Hymenoptera, therefore, the sucking pump is a cibario-pharyngeal structure; in Hemiptera and Diptera the pump is purely cibarial.

The capacious pharyngeal section of the pump has no effective dilator apparatus, since only three pairs of small muscles (fig. 10 C, 34, 35, 36) attach on it from the head wall. On its posterior surface two groups of long slender fibers (38), arising laterally on the tentorial bridge (TB), spread downward, going beneath the circular





A discussion of the working mechanism of the sucking pump without observations on the action of the organ in a living bee could be but little convincing, and will not be attempted here, except to point out that the cibarial section, with its strong equipment of dilator and compressor muscles, must be the active pumping apparatus, or true *suctorium*. With the bee, however, an important function of the feeding mechanism is regurgitation. It is probable, therefore, that the pump is capable of reversing its action according as the occasion demands an intake or an output of food material.

## II. THE PROTHORAX

The prothorax of the bee, as of most other clistogastrous Hymenoptera, is not an anatomical unit because of the close association of the pronotum with the pterothorax, and the independence of the prothoracic pleurosternal complex, or *propectus*, which serves as a suspensorium for the first legs and as a support for the head.

*The pronotum.*—The notal plate of the prothorax is a collarlike sclerite closely fitted on the anterior end of the mesothorax (fig. 15,  $N_1$ ). Since its tapering lower ends meet on the venter, though they do not unite (fig. 11 A), the pronotum forms a sclerotic annulus interpolated between the pleurosternal parts of its own segment and the mesothorax. The lateral areas of the pronotum are produced posteriorly into a pair of spiracular lobes (*spl*) that cover depressions of the mesothorax and conceal the first spiracles on their inner surfaces. The posterior pronotal margin dorsally is sharply and deeply inflected with the anterior margin of the mesonotum (fig. 11 F); from the latter depends a small prephragma (*1Ph*), but the pronotum is separated from the base of the phragma by a narrow line of intersegmental membrane (*Mb*).

*The propectus.*—The pleurosternal region of the prothorax is merged with the neck in a prenatal cone (fig. 15), which is partly overlapped posteriorly by the pronotum and tapers forward to its connection with the foramen magnum on the back of the head. The dorsal wall of the cone is the dorsal neck membrane, which is uninterrupted from the head to the pronotum; the lateral and ventral walls contain the pleural and sternal plates of the prothorax, which together constitute the propectus (fig. 11 G).

Each prothoracic pleuron is an elongate triangular plate (fig. 11 C), the anterior apical part of which tapers into a mesally bent *occipital process* (C, E, *e*) that articulates with the corresponding occipital condyle of the head (B), and which, therefore, would appear to

represent a cervical sclerite fused with the pleuron. On the lower posterior angle of the pleural plate is articulated the coxa of the first leg (C, *Cx*). From the coxal articulation there extends upward close to the posterior pleural margin a groove (*pls*), which is the *pleural sulcus*, since it runs into the base of the large internal *pleural apophysis* (*PLA*). The groove sets off a very narrow posterior *epimeral strip* (*Epm*) of the pleuron from a large anterior *episternal region* (*Eps*).

Internally the episternum presents close to its upper margin a wide, shelflike *horizontal apodeme* (fig. 11 E, *c*) inflected from a submarginal groove on its outer surface (C, *b*). The horizontal apodeme expands anteriorly into a large mesal lobe (C, E, *d*), termed by Duncan (1939) in the wasp the "posterior ramus of the occipital process," but which, since it gives attachment to several muscles that are in most insects inserted on a distinct neck sclerite, may appropriately be named the *cervical apodeme*. The cervical apodeme and the pleural apophysis form prominent points of muscle attachments at opposite ends of the pleuron.

The prosternum lies ventrally between the pleural plates and the bases of the coxae (fig. 11 G). It is differentiated by a narrow constriction into a wide, triangular, anterior *basisternal region* (*Bs*) flanked by the episterna, and a narrow, elongate, posterior *furcasternal region* (*Fs*) lying between the coxae. The furcasternum bends upward at a steep angle from the horizontal basisternum (I), and carries an elaborate endoskeletal structure, the *prothoracic endosternum*. Externally the furcasternum is featured by a median groove (K, *f*), and by a pair of posterior pits (*g*) that mark the roots of the sternal apophyses.

*The prothoracic endosternum.*—The large endoskeletal structure supported on the sternum of the prothorax occupies much of the interior of the segment (fig. 11 B, E, *Endst*) and gives attachment to various muscles (fig. 12 B, C). Structurally the endosternum includes a supporting base on the furcasternum, a pair of laterally divergent dorsal wings, and a horizontal bridge between the wings. The sternal support consists of a vertical median plate (fig. 11 I, *h*) inflected from the median groove of the furcasternum, which posteriorly is reinforced by a pair of lateral thickenings (*i*) arising from the posterior furcasternal pits, and anteriorly tapers into a low ridge that runs out on the basisternum (*j*). The endosternal wings are a pair of plates with thickened anterior margins diverging from the basal ridge (J, *k, k*) in a forward direction because of the upward slant of the furcasternum in the natural position (I). The bridge is a wide,

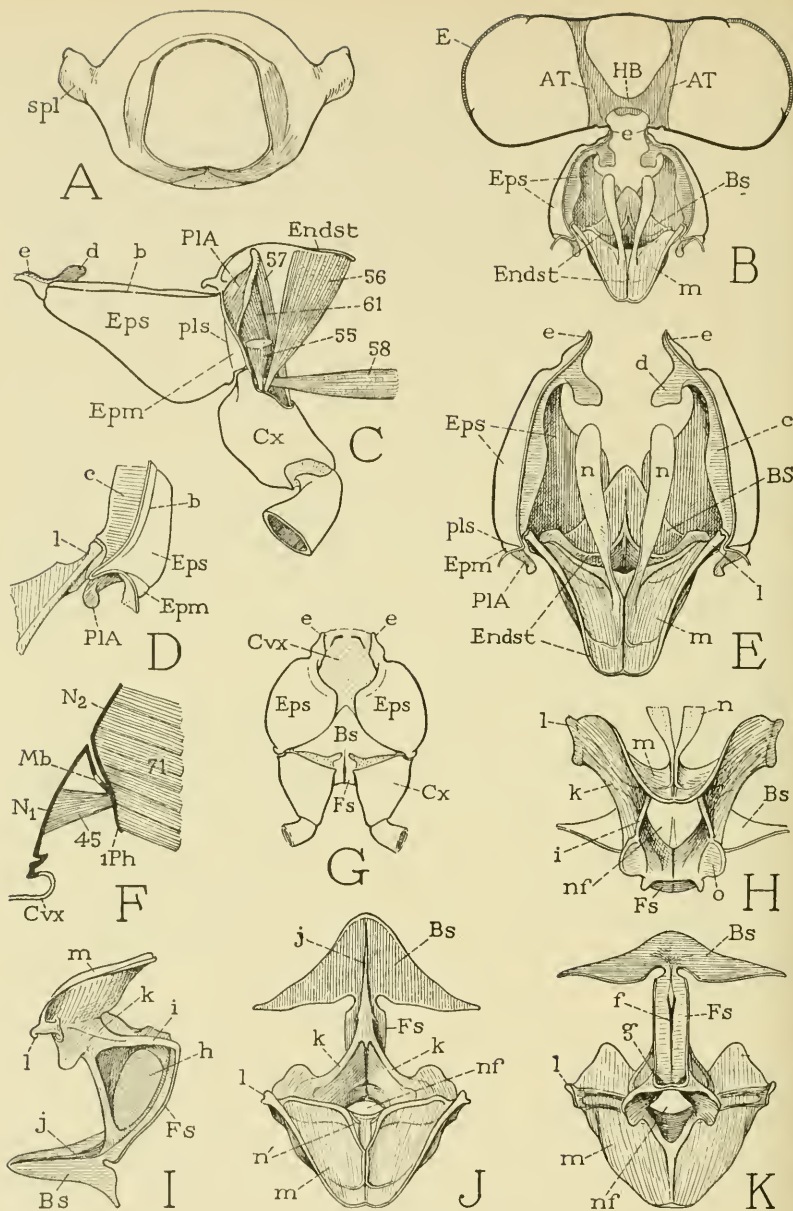


FIG. 11.—The prothorax (drone).

A, pronotum, anterior view. B, pleurosternal parts of prothorax and horizontal section of attached head, dorsal view. C, propleuron and base of first leg, left side. D, articulation of lateral arm of endosternum with propleuron and base of first leg, dorsal view. E, pleurosternal and endosternal skeleton of prothorax, dorsal view. F, median section of pronotum and adjacent part of mesonotum, showing first phragma (*iPh*) to be a prephragma of mesonotum, separated from pronotum by narrow membrane (*Mb*). G, pleurosternal parts of prothorax and bases of first legs, ventral view. H, prosternum and endosternum, posterior view. I, same, natural position, lateral view. J, same, anterodorsal view. K, same, ventral view, furcasternum horizontal.

*b*, submarginal groove of episternum; *c*, horizontal apodeme of episternum along line of external groove *b*; *d*, cervical apodeme of episternum; *e*, occipital process of episternum; *f*, median groove of furcasternum; *g*, posterior pit of furcasternum; *h*, median basal plate of endosternum; *i*, thickened posterior edge of wing plate of endosternum; *j*, median ridge of basisternum; *k*, *k*, divergent wing plates of endosternum; *l*, lateral extremity of endosternum; *m*, supraneural bridge of endosternum; *n*, apodeme of muscle 51; *n'*, base of *n*, cut off; *o*, attachment lobe of muscle 52.



scoop-shaped plate, broad anteriorly, tapering and rounded posteriorly (I, J, *m*), set approximately horizontally on the upper edges of the wing plates. The space between the wings is thus converted by the bridge into a short channel, which gives passage to the nerve cords, and hence may be termed the *neural foramen* (H, J, K, *nf*). The lateral extremities of the bridge (*l*) are closely articulated with the posterior angles of the horizontal apodemes of the episterna (D, E).

The prothoracic endosternum of the bee does not have the structure of an ordinary Y-shaped sternal "furca," in which the divergent arms are the primary sternal apophyses carried inward by a median sternal inflection that forms the stalk of the fork. In the bee the posterior lateral thickenings that brace the median plate (fig. 11, H, I, *i*) appear to be independent ingrowths from the furcasternum and evidently represent the usual pair of sternal apophyses, which, while retaining their bases on the sternum, have united with the posterior end of the median plate. The supraneural bridge may be regarded as a secondary formation produced by the union of flat mesal outgrowths from the divergent wing plates.

Various aspects of the prothoracic endosternum are shown in figure 11. At B and E the endosternum is seen in place within the prothorax, with its lateral extremities articulating against the pleura. H gives a posterior view looking through the neural foramen, only the posterior end of the upturned furcasternum being visible. At I the endosternum and sternum are shown from the left side, the basisternum being horizontal, the furcasternum steeply ascending. J gives an antero-dorsal view of the same parts, showing the endosternal wings diverging upward from the median basal ridge and united by the supraneural bridge. At K the sternum and endosternum are shown from below as seen when the furcasternum is turned horizontally.

*The prothoracic muscles.*—The musculature of the prothorax comprises (1) muscles that move the head directly, (2) dorsal and ventral intersegmental muscles between the prothorax and the mesothorax, (3) muscles that move the propleura, or the entire propectus, which probably effect indirectly movements of the head, and (4) muscles of the legs.

The direct muscles of the head are attached on the margins of the foramen magnum, not in the usual manner on a postoccipital ridge. They include four pairs of levator muscles and one pair of depressor muscles. Two pairs of the levators take their origins on the prephragma of the mesothorax (fig. 12 A), one pair (40) being median, parallel, and inserted on the head laterad of the apical notch of the foramen magnum (B, 40), the other pair (A, 41) lateral in origin,



convergent beneath the first, and inserted in the apical notch of the foramen (B, 41). The third pair of levators are large three-branched muscles arising by broad bases on the episterna (D, 42), one branch of each muscle (42a) above the horizontal apodeme of the episternum (*c*), the second (42b) on the side below the apodeme, the third (42c) on the ventral expansion; the three branches converge to a strong tendon attached in the laterodorsal notch of the foramen (B, 42a,

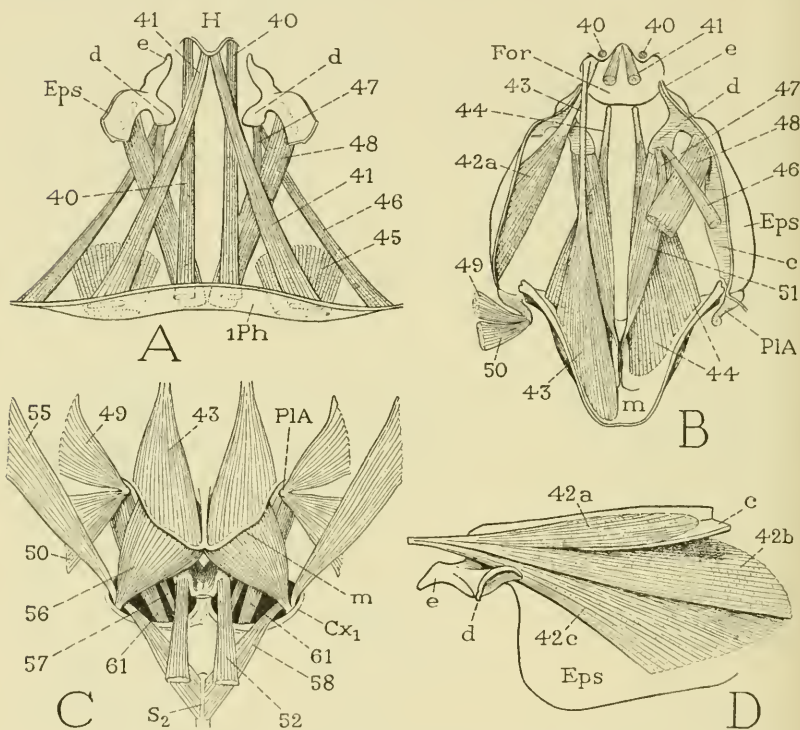


FIG. 12.—Muscles of prothorax (drone).

A, dorsal muscles, ventral view. B, ventral and lateral muscles, dorsal view. C, muscles of endosternum and fore coxae, posterior view. D, branches of cephalic muscle 42 arising on inner face of proepisternum.

*c*, horizontal apodeme of episternum; *d*, cervical apodeme of episternum; *e*, occipital process of episternum; *m*, supraneural bridge of endosternum.

only one branch, on the left side, shown in this figure). The fourth pair of head levators arises posteriorly on the dorsal surface of the supraneural bridge of the endosternum (B, C, 43), the fibers of each muscle converging to a long, thick tendon attached on the head just laterad of the pleural levator (B, 43). The depressors of the head are a pair of large two-branched muscles (B, 44) arising on the

supraneural bridge beneath the endosternal levators (43), and inserted by strong tendons on the lower margin of the foramen magnum. Duncan (1939) describes the two branches of this muscle in *Vespula* as first and second depressors of the head, but adds that the two might be considered subdivisions of a single muscle.

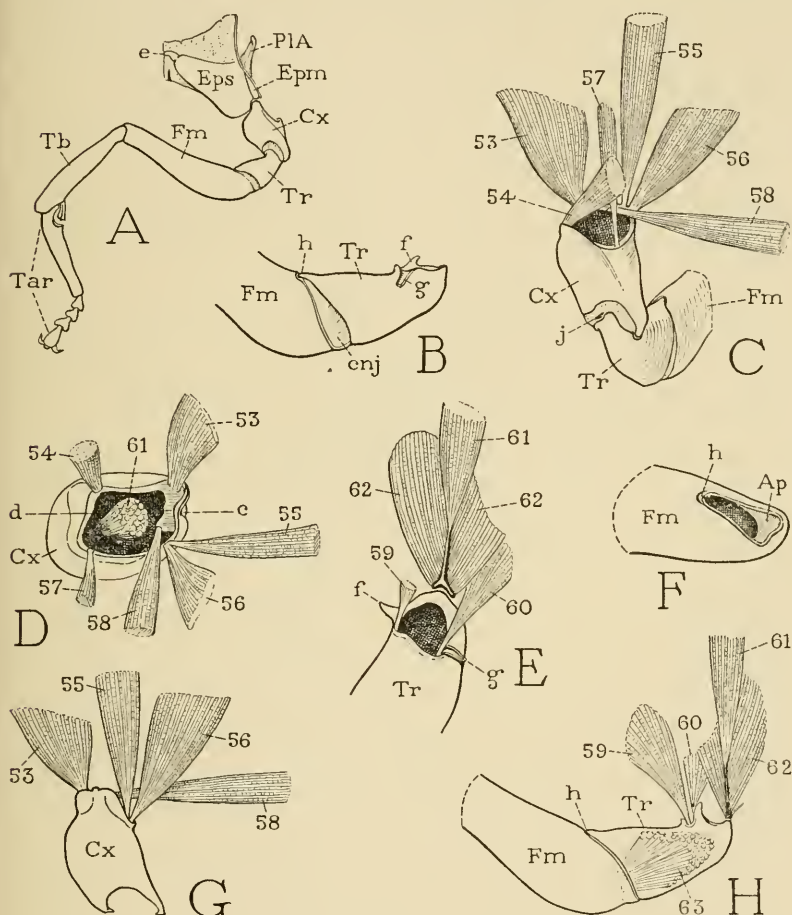


FIG. 13.—The prothoracic leg (drone).

A, left half of propleuron, and left fore leg, lateral view. B, trochanter and base of femur of left leg, posterior view. C, base of right leg and coxal muscles, mesal view. D, base of right coxa with muscles, dorsal view. E, base of left trochanter with trochanteral muscles, dorsal view. F, base of right femur, anterodorsal view. G, left coxa with lateral muscles, lateral view. H, right trochanter and base of femur with muscles, anterior view.

c-d, axis of pleurocoxal articulation; e, occipital process of episternum; f, anterior coxo-trochanteral articulation; g, posterior coxo-trochanteral articulation; h, dorsal trochantero-femoral articulation; j, base of depressor apodeme of trochanter.

The dorsal and ventral intersegmental muscles of the prothorax are, respectively, intertergal and intersternal. The dorsal muscles are two large bundles of fibers (fig. 12 A, 45) arising anteriorly by broad bases on the pronotum (fig. 11 F), and tapering somewhat to their posterior attachments on the prephragma of the mesonotum (*1Ph*). The contraction of these muscles would appear to depress the pronotum in the bee, though in *Vespula* two pairs of corresponding muscles are regarded by Duncan (1939) as retractors of the mesonotum in opposition to the dorsal muscles of the mesothorax. The ventral intersegmental muscles (fig. 12 C, 52) have their anterior attachments on a pair of small lobes of the apophyseal components of the prothoracic endosternum (fig. 11 H, *o*), and their posterior attachments on two small anterior tonguelike processes of the supraneural bridge of the pterothoracic endosternum (figs. 22 C, 24 A, 52). These muscles are evidently retractors of the propectus.

The muscles of the propleura comprise tergal and endosternal muscles inserted on the anterior parts of the episterna, and tergal muscles inserted on the extremities of the pleural apophyses. The largest of the propleural muscles (fig. 12 A, 48) arise close together on the posterior inflection of the pronotum and diverge forward above the dorsal muscles of the head to the anterior ends of the horizontal apodemes of the episterna. A second, slenderer pair (46) arises laterally on the prephragma of the mesonotum and converges anteriorly to the cervical apodemes (*d*). Inserted close to the latter muscles on each side is another small muscle (47), which may be a branch of 48 since its fibers appear to follow those of this muscle from the pronotum. A fourth pair, two large sternopleural muscles (fig. 12 B, 51), arises from the long, straplike apodemes of the supraneural bridge of the endosternum (fig. 11 E, *n*), and diverges forward to the cervical apodemes of the pleura (fig. 12 B, *d*). The tergopleural muscles inserted on the pleural apophyses include two fan-shaped muscles on each side (fig. 12 C, 49, 50) arising anteriorly on the side of the pronotum, and converging posteriorly to the upper extremity of the apophysis. These muscles clearly are protractors of the propectus, their antagonists being the ventral intersegmental muscles (52).

The strength of the anterior pleural musculature of the prothorax suggests that movement of the pleural plates has some important purpose. The head, being articulated on a transverse axis between the occipital processes of the episterna (fig. 11 B), can have only a tilting movement on the thorax by the action of its own levator and depressor muscles; but the pleural plates, by reason of their lack of fixity on the

sternum, their posterior articulations on the endosternal arms, and the shortness of the occipital axis between their anterior ends (fig. 11 B, *e*), are well adapted to give partial rotary movements to the head by a differential, or antagonistic, action of the right and left sets of muscles attached on their anterior parts.

The prothoracic leg muscles will be described in connection with the structure of the legs.

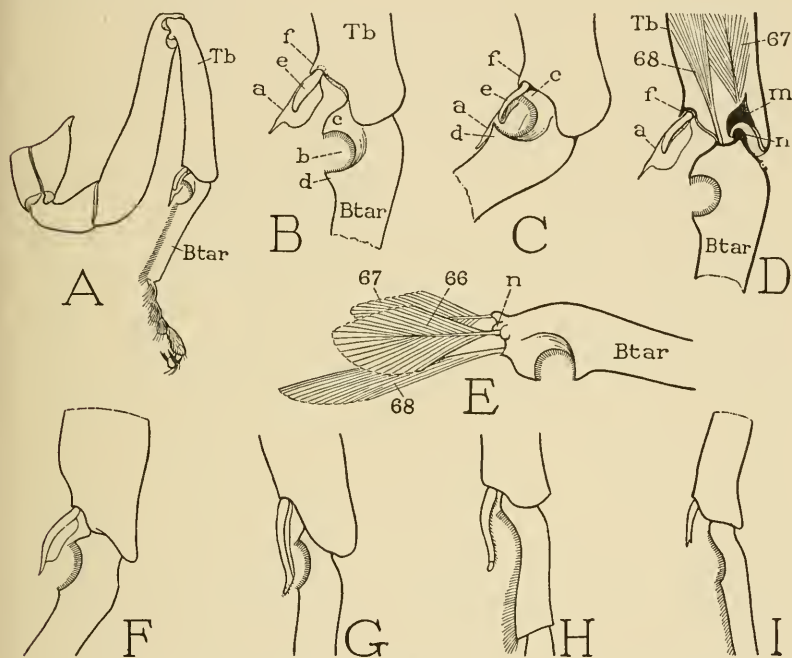


FIG. 14.—The antenna cleaner and the tibio-tarsal joint of the fore leg.

A, left fore leg of worker bee, showing antenna cleaner at base of first tarsomere (Btar). B, antenna cleaner open, anterior view. C, antenna cleaner closed. D, tibio-tarsal joint with muscles exposed by removal of anterior wall of tibia. E, base of first tarsomere with muscles, anterior view. F, antenna cleaner of *Halictoides calochorti* Ckll. G, same of *Vespa maculata* (L.). H, same of *Troglodytes vulpinus* (Grav.). I, same of *Orussus sayi* Westw.

*a*, closing lobe (fibula) of antenna cleaner; *b*, tarsal notch of antenna cleaner; *c*, basal angle of notch; *d*, distal angle of notch; *e*, anterior lobule of closing lobe; *f*, stop-process of tibia; *m*, tibial articular process; *n*, tarsal articular process.

### III. THE PTEROTHORAX

The wing-bearing section of the trunk in the clistogastrous Hymenoptera (fig. 15) is composed of the three body segments that are the mesothorax, the metathorax and the first abdominal segment of other insects. Though the notal plate of the prothorax ( $N_1$ ) is closely associated with the pterothorax, and looks like a collar on the



front of the mesothorax, its connection with the latter is for its own security, since the pronotum serves principally for the attachment of prothoracic and head muscles, and takes no part in the pterothoracic mechanism. The pterothoracic segments, on the other hand, are intimately united to form a mechanical unit supporting the wings, the first and second legs, and the abdomen. Between the third pterothoracic segment, known as the *propodeum*, and the abdomen is a deep constriction, which allows the abdomen to be freely movable on the thorax.

On the dorsum of the pterothorax the segmental plates are well defined, and behind the pronotum (fig. 15  $N_1$ ), the mesonotum ( $N_2$ ), the metanotum ( $N_3$ ), and the propodeal tergum (*IT*) can readily be identified. On the venter (fig. 16 F) the sternal areas of the mesothorax ( $S_2$ ) and the metathorax ( $S_3$ ) are separated by a distinct groove between the bases of the middle legs, and the propodeal sternum (*IS*) is an independent sclerite behind the third legs, but laterally there is no demarcation between the sternal and pleural areas in either the mesothorax or the metathorax (fig. 15). The structure of the pleural region of the pterothorax is difficult to interpret, because neither the grooves nor the areas distinctly set off by the latter appear to conform with the pleural pattern of generalized insects.

*The mesonotum.*—The back plate of the mesothorax (fig. 15,  $N_2$ ) covers the strongly convex upper and anterior parts of the pterothorax, and is completely divided by a transverse fissure (*sf*) into two plates. For practical description the two plates are commonly called the "scutum" and the "scutellum," but the line of division does not conform with the sulcus that separates the scutellum from the scutum in generalized insects. The true scutoscutellar sulcus in the bee is marked internally by a strong, arched *notal ridge* (fig. 16 D, *NR*), which on the middle of the back is coincident with the groove between the two mesonotal plates, but laterally follows a groove (fig. 15, *ns*) that curves posteriorly and sets off before it on each side an elongate oval or lenticular area (*sct*) which properly belongs to the scutum. The mesonotum of the bee and of related Hymenoptera, therefore, is secondarily divided into two major parts without regard to the original differentiation into scutum and scutellum by the external sulcus (*ns*) of the notal ridge. The true scutellum forms the prominent swelling on the highest part of the back ( $Scl_2$ ) and tapers laterally to the posterior angles of the mesothoracic wing bases; the scutum ( $Sct_2$  and *sct*) covers the entire anterior rounded surface of the back between the notal sulcus (*ns*) and the pronotum, and supports the greater



part of the wing bases on its sides. In a study of the mechanism of the thorax rather than its morphology, however, it will be better to follow the mechanical pattern of the structure, in which the mesonotum consists of an *anterior notal plate* and a *posterior notal plate*. The reason for the division of the notum into these two plates will be clear when we study the wing mechanism.

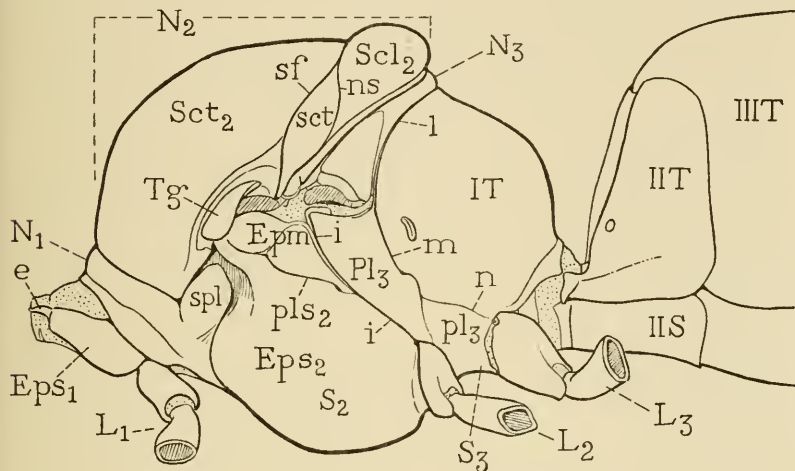


FIG. 15.—The thorax and the base of the abdomen (drone), left side, wings removed.

*e*, occipital process of proepisternum; *Epm*, epimeron of mesopleuron; *Eps*<sub>1</sub>, prothoracic episternum; *Eps*<sub>2</sub>, mesothoracic episternum; *i*, groove between mesopleuron and metapleuron; *IIS*, sternum of first abdominal segment; *IIT*, *IIIT*, tergal plates of first and second abdominal segments; *IT*, tergal plate of propodeum; *l*, groove between metanotum and propodeum; *L*<sub>1</sub>, *L*<sub>2</sub>, *L*<sub>3</sub>, legs; *m*, *n*, groove between metapleuron and propodeum; *N*<sub>1</sub>, pronotum; *N*<sub>2</sub>, mesonotum; *N*<sub>3</sub>, metanotum; *ns*, primary notal sulcus between scutum and scutellum; *Pl*<sub>3</sub>, *pls*<sub>2</sub>, upper and lower parts of metapleuron; *pls*<sub>2</sub>, pleural sulcus of mesothorax; *S*<sub>2</sub>, mesosternum; *S*<sub>3</sub>, metasternum; *Scl*<sub>2</sub>, scutellum of mesonotum; *Sct*<sub>2</sub>, scutum of mesonotum; *sct*, posterolateral subdivision of mesoscutum; *sf*, scutal fissure; *spl*, spiracular lobe of pronotum; *Tg*, tegula.

The anterior mesonotal plate (figs. 15, 16 C, *Sct*) is a large, shield-shaped sclerite (fig. 16 B) convex dorsally and strongly declivous anteriorly. Its front margin is deflected into the relatively small prephragma (*rPh*), and on its lateral margins are the *anterior notal wing processes* (*ANP*). The posterior, scutoscuteellar mesonotal plate (figs. 15, 16 C, *Scl*, *sct*) is somewhat crescent-shaped as seen from above (fig. 16 A) or below (D) with the concave margin anterior; internally it is braced by the strong scutoscuteellar notal ridge (D, *NR*). The lateral scutal areas of the plate bear the *posterior notal wing processes*, and the tapering ends of the scutellar

area give attachment to the *axillary cords* of the wing bases. The posterior margin is deeply inflected laterally in the groove before the metanotum, and is here connected with the arms of the mesothoracic postphragma (fig. 16 C, D, G, *2Ph*).

The phragmata of the insect thorax are primarily infoldings or ingrowths of the body wall on the intersegmental lines between the successive notal plates, but in the bee the first phragma is solidly united with the anterior margin of the mesonotum, and thus becomes a mesothoracic *prephragma*, while the close association of the second phragma with the posterior margin of the mesonotum gives this phragma the status of a mesothoracic *postphragma*. A third phragma, usually present between the metanotum and the first abdominal segment, is absent in the bee. The phragmata serve to give increased surfaces of attachment for the intersegmental dorsal muscles, but when two successive phragmata are united with opposite ends of the same segmental plate, the muscles become intrasegmental in their action.

The prephragma of the mesothorax of the bee is a simple, crescent-shaped ingrowth from the deflected anterior margin of the scutum (fig. 16 B, *1Ph*), separated by a narrow line of intersegmental membrane (fig. 11 F, *Mb*) from the overlapping pronotum. The postphragma, on the other hand, is a large U-shaped sclerite (fig. 16 D, *2Ph*) projecting far back under the metanotum into the cavity of the propodeum. Its only connections with the mesonotum are the attachments of its basal arms with the lateral ends of the scutellum. The base of each arm splits into an outer and an inner lamella (G); the inner lamella (*v*) is continuous with an infolding of the mesoscutellar margin, the outer lamella (*u*) is reflected back into the anterior margin of the metanotum. The postphragma thus maintains its intersegmental relations, but there is in the bee no representative of the usual postscutellar supporting plate, or postnotum, other than the exposed parts of the inner lamellae of the phragma where the latter join the mesoscutellum.

*The metanotum.*—The back plate of the metathorax is a narrow transverse sclerite (fig. 16 E), constricted mesally and expanded laterally, closely interpolated between the mesonotum and the propodeum (fig. 15, *N<sub>3</sub>*). The metanotum shows no division into scutum and scutellum, but its widened lateral parts form a prominent triangular area on each side. From the lateral margin of each triangular area there is deflected an irregular, semidetached sclerite (fig. 21 E, *n<sub>3</sub>*), and before the latter is a smaller independent sclerite (*d*), both of which sclerites give support to the wing base, as will

be described later. The metanotum is separated from the propodeum by a prominent groove (fig. 15, *l*), which forms a low ridge internally, but there is no metathoracic postphragma.

*The propodeum.*—The dorsal region of the propodeum (fig. 15, *IT*) is a large, strongly convex plate covering the posterior part of the pterothorax, containing the spiracles of its segment laterally, and posteriorly descending steeply to the petiole of the abdomen. This plate, commonly termed the "propodeum," is really the propodeal tergum, the sternum of the propodeal segment being a narrow ventral plate behind the bases of the third legs (fig. 16 F, *IS*).

*The pterothoracic pleura.*—The pleuron of a wing-bearing segment in most insects is differentiated into an anterior *episternum* and a posterior *epimeron* by a groove, the *pleural sulcus*, which extends upward from the coxal articulation to the wing base, and forms internally a strong *pleural ridge*, which bears an apodemal process, or *pleural apophysis*, associated with the extremity of the endosternal arm of the corresponding sternum. In the bee this structural pattern of the pleuron is obscured in both the mesothorax and the metathorax.

The mesopleural area of the honey bee is well defined anteriorly and posteriorly by deep grooves separating it from the prothoracic notum in front and the metathoracic pleuron behind (fig. 15), its "free" upper margin borders the subalar membrane, ventrally, however, as already noted, the lateral sclerotization of the segment is continuous to the midline of the venter (fig. 16 F), and there is nothing to mark the transition from pleuron to sternum, except the ventral attachment of the huge dorsoventral muscle of the mesothorax (fig. 16 C, 72), which is assumed to arise on the sternum.

The upper part of the mesopleuron is crossed by an oblique groove (fig. 15, *pls<sub>2</sub>*), which appears to be the pleural sulcus, separating a small upper epimeral area (*Epm*) from a large lower episternal area (*Eps*). The groove contains near its posterior end a conspicuous pit (fig. 17 A, *pla*) that forms internally a small pleural apophysis (B, *PlA*) intimately associated with the mesothoracic arm of the pterothoracic endosternum (G, *PlA*, *SA<sub>2</sub>*). Furthermore, the line of the posterior part of the groove is marked internally by a strong ridge (B, *PlR*) bearing the apophysis. These several features almost certainly identify the oblique groove (A, *pls*) as the true pleural sulcus of the mesothorax. Beyond the apophysis the sulcus merges with the intersegmental groove (fig. 15, *i*) that runs downward to the pleural articulation of the middle coxa. A second groove of the pleuron (fig. 17 A, *e*) arises near the middle of the pleural sulcus, runs upward and posteriorly through the epimeral region, cutting the

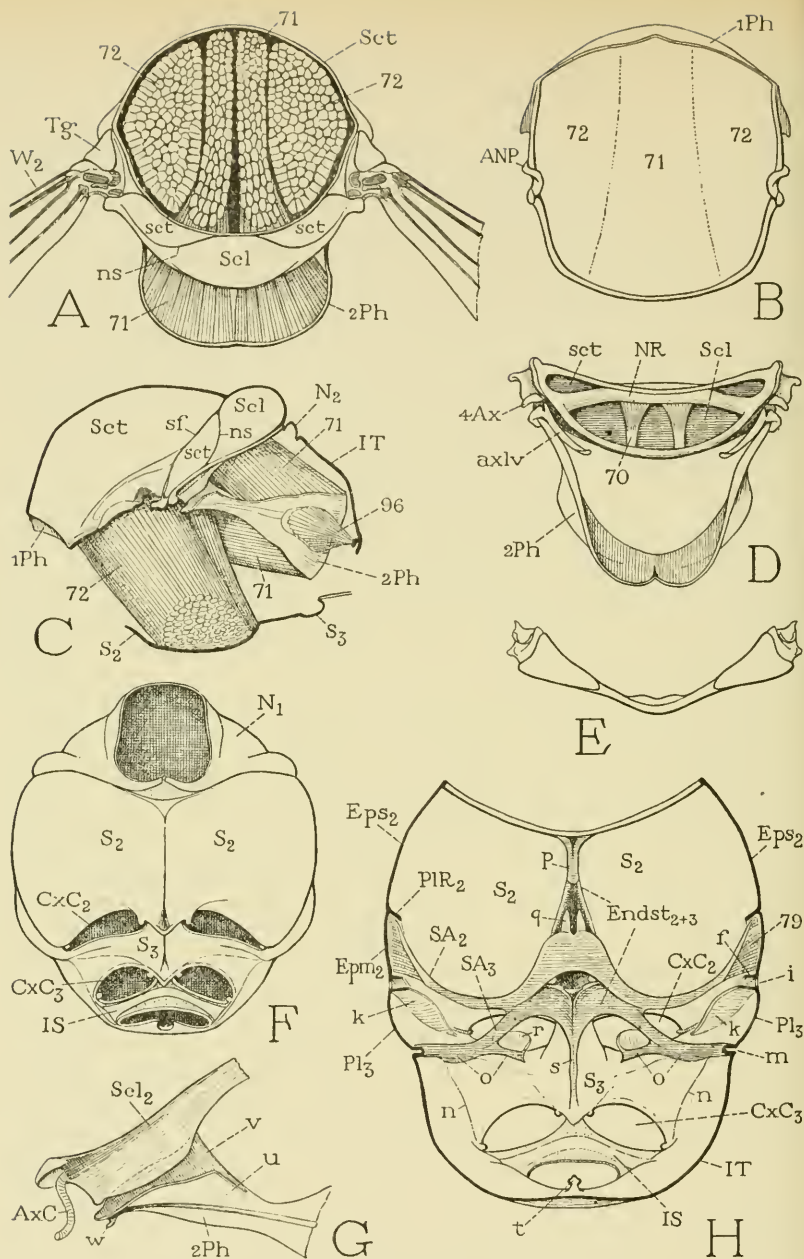


FIG. 16.—Dissection of the pterothorax (drone).

A, mesothorax and wing bases, dorsal view, with most of scutal area removed exposing ends of longitudinal and dorsoventral muscles. B, major scutal plate of mesothoracic notum, ventral view. C, pterothorax with pleural and propodeal walls removed on left side, showing phragmata and muscles. D, posterior notal plate of mesothorax and attached second phragma, ventral view. E, metanotum, dorsal view. F, ventral surface of thorax, legs and propectus removed. G, left lateral arm of mesoscutellum and corresponding stalk of second phragma, lateral view. H, ventral half of pterothorax, dorsal view, showing endoskeletal structures.

*f*, posterior marginal ridge of mesopleuron; *i*, conjunctiva between mesopleuron and metapleuron; *k*, anterior inflection of metapleuron; *m*, groove between metapleuron and propodeum; *n*, line of external groove *n* (fig. 15); *ns*, notal sulcus; *o*, ridge of external groove *m* (fig. 15); *p*, process of mesosternal ridge giving attachment to muscle 58 (fig. 22C); *q*, process of supra-neural bridge of endosternum giving attachment to muscle 52 (fig. 22C); *r*, lobe of ridge *o* giving attachment to basalar muscle of metathorax (fig. 21H, 101); *s*, median ridge of metasternum; *sf*, scutal fissure; *t*, median process of propodeum giving attachment to muscles 96 (C, and fig. 27C); *u*, *v*, outer and inner lamellae of basal stalk of second phragma; *w*, articular process on stalk of second phragma for axillary lever.



latter into two parts (*Epm*, *epm*), and then turns downward close to the posterior epimeral margin, and, along with the pleural sulcus, finally becomes lost in the intersegmental groove. This recurrent groove also forms a strong internal ridge (*B*, *f*), and it too has been regarded as the pleural sulcus (see Snodgrass, 1925), but it has none of the distinctive features of the latter. Duncan (1939) gives the same interpretation of the pleural structure in *Vespula* as is given here for *Apis*. The obliteration of the lower part of the mesepimeron makes it appear that the middle coxa (fig. 15) has an intersegmental pleural articulation, though its ventral articulation is with the mesosternum (fig. 16 F).

Anteriorly the mesopleuron presents a deep concavity (fig. 17 A, *c*), which is covered by the spiracular lobe of the pronotum (fig. 15 *spl*); its dorsal margin forms a long elevation, on the anterior part of which (fig. 17 A, *d*) articulates the basalar sclerite (fig. 19 B, *Ba*), and on the posterior part (*WP*) the second axillary of the wing base (*2Ax*). Behind the wing process (*WP*) the descending margin of the epimeron is inflected mesally in a wide plate (fig. 17 B, *Epm'*) supported on the ridge (*f*) of the recurrent suture. The inner edge of this inflected plate carries an elongate sclerite (*G*, *h*), attached posteriorly to the base of the postphragma (fig. 19 I), which supports the small subalare (*Sa*).

The inner surface of the mesopleuron presents an unusual structure (fig. 17 B). From its anterior and upper margin, between the first spiracle and the wing process, there is reflected posteriorly a large plate (*g*), the lower part of which is bridged to both the pleural ridge (*PIR*) and the recurrent ridge (*f*) by a strong arch. Between this plate and the outer pleural wall is a flat pocket open above and below the bridge (as indicated in the figure by an arrow), which lodges one of the muscles of the third axillary sclerite of the wing base (*E*, 76*a*). Behind the upper part of the pocket is seen the inflected external plate of the epimeron (*B*, *Epm'*) united with the recurrent ridge (*f*). The thick pleural ridge (*PIR*) ends posteriorly in the small pleural apophysis (*PLA*).

The metathoracic pleuron is a narrow, oblique plate on the side of the pterothorax (fig. 15), extending from the wing base above to the hind coxa below, between the mesopleuron and the propodeum. It is divided by a groove into a larger upper part (*Pl<sub>3</sub>*) and a smaller lower part (*pl<sub>3</sub>*), but the latter is continuous ventrally with the metasternum (*S<sub>3</sub>*). The dorsal plate (fig. 21 C, *Pl<sub>3</sub>*) supports on its upper margin the basalar (*Ba*), the second axillary (*2Ax*), and the small subalare (*Sa*) of the metathorax; it includes, therefore, in its upper part at



least, both the episternum and the epimeron, though a separating sulcus is not present. The anterior pleural margin is inflected in a high apodemal ridge (figs. 16 H, 21 C, *k*); posteriorly the upper pleural plate is limited by a deep groove (fig. 15, *m*) separating it from the propodeum, which forms a strong internal ridge (fig. 16 H, *o*) with which the endosternal arm of the metathorax (*SA*<sub>3</sub>) is fused. From the lower part of the groove *m* (fig. 15) a weak impression (*n*) goes posteriorly to the coxal articulation. It is evident, therefore, that the epimeron of the metathorax, as that of the mesothorax, has been mostly eliminated, and that the apparent intersegmental groove (*m*, *n*) before the propodeum includes the lower part of the pleural sulcus extending to the coxal articulation. The position of the posterior pleural muscles behind this groove and its internal ridge confirms the above interpretation.

*The thoracic spiracles.*—Of the three pairs of spiracles on the thorax those of the first pair are of particular interest because of their size, position, and structure. They are contained in the membranous inner walls of the spiracular lobes of the pronotum (fig. 17 C, *1Sp*), and therefore open toward the body into the depressions of the mesopleura (A, *c*) beneath the lobes, the entrances to which are guarded by dense fringes of plumose hairs on the lobe margins. The reflected lower margin of each pronotal lobe is supported on a small, rectangular cartilagelike plate (D, *a*) arising from a lobe of the anterior margin of the mesopleuron (A, B, *b*). The plate is a thickening of the intersegmental membrane, and serves to prevent movement of the spiracular lobe. The orifice of each spiracle (C, F) is a simple opening in the spiracular membrane leading into a large tracheal trunk (*Tra*) going forward into the prothorax. Above the aperture is an oval plate (F, *Op*), the ventral edge of which forms the upper lip of the aperture; the lower lip is merely the soft edge of the surrounding membrane. The plate can be pulled down over the aperture by a slender muscle (73) and thus serves as a closing lid, or *operculum*, of the spiracle. The occlusor muscle arises from a small knob on the anterior margin of the mesopleuron (C, 73), and is inserted by a tendon in the membrane close to the anterior margin of the spiracular orifice (F), not directly on the operculum. The simple closing apparatus of this spiracle would appear to be more effective in blocking the entrance of air into the trachea than for preventing its egress, but the soft lower lip of the closed aperture is easily pushed inward, and probably gives little resistance to parasitic mites seeking an entrance.

The second spiracles lie below the wings in the membrane concealed between the upper edges of the mesothoracic and metathoracic pleura. They are minute apertures without a closing apparatus, and have been

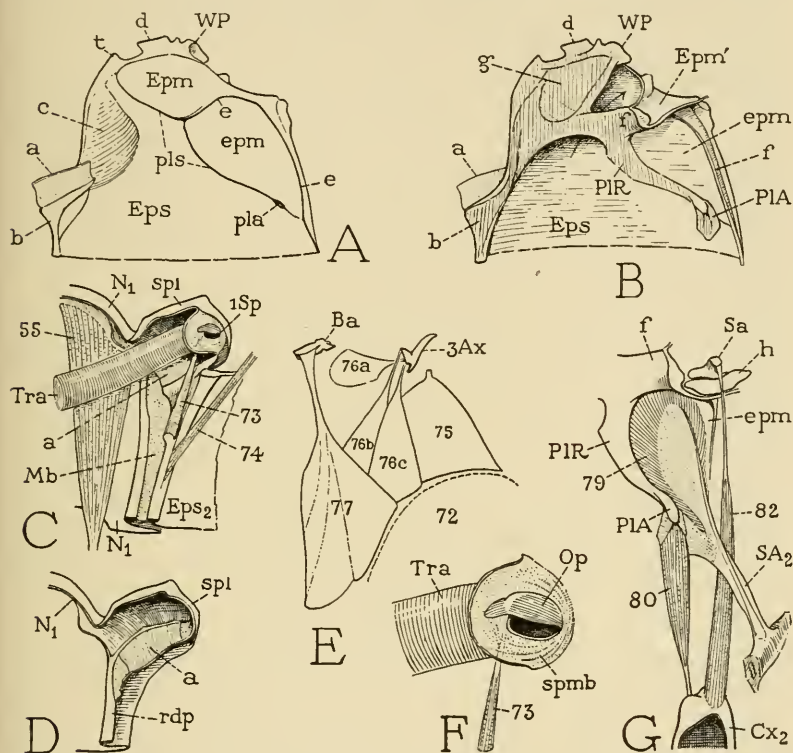


FIG. 17.—The mesopleuron and the first spiracle (drone).

A, left mesopleuron, lateral view. B, right mesopleuron, mesal view. C, right first spiracle and adjoining parts of prothorax and mesothorax, mesal view. D, right spiracular lobe of pronotum, mesal view. E, mesopleural muscles arising on episternum, right side, mesal view. F, right first spiracle and connected trachea, mesal view. G, posterior pleural muscles of mesothorax, right side, mesal view.

a, platelike thickening of intersegmental membrane connecting spiracle lobe of pronotum with mesepisternum; b, lobe of mesepisternum supporting a; c, depression of mesepisternum covered by spiracular lobe of pronotum; d, lobe of mesepisternum supporting basalare; e, recurrent groove of mesopleuron; f, internal ridge of recurrent groove; g, mesal inflection of mesopleuron continuous with pleural ridge (PIR); h, epimeral plate supporting subalare; t, point at which mesoscutum is supported on pleuron.

observed by the writer only in the worker. The third spiracles are those of the propodeum, and have the structure of the other abdominal spiracles. Each is provided with a short occlusor muscle (fig. 27 B, 122) stretched between the two ends of the spiracle, and

with a long slender dilator muscle (123) arising ventrally from a small knob on the pleural margin of the metacoxal cavity just before the pleural coxal process ( $CxP_3$ ).

*The pterothoracic sternal areas.*—The ventral surface of the pterothorax is entirely sclerotized except in the propodeal region (fig. 16 F), and the sternal areas of the mesothorax and the metathorax ( $S_2$ ,  $S_3$ ), though separated from each other by a groove between the bases of the middle legs, are in each segment continuous with the pleural areas (fig. 15). The lateral extent of the mesosternum can be judged only by the areas occupied by the ventral ends of the great pillars of dorsoventral muscles (fig. 16 C, 72), which muscles in generalized insects have their ventral attachments on the sternum; in the bee the bases of these muscles extend well up on the sides of the pleurosternal areas. In the metathorax there are no corresponding tergo-sternal muscles, but the sternal area of this segment may be regarded as that part of the venter lying between and before the hind legs ( $F$ ,  $S_3$ ). Both the mesosternal area and the metasternal area are marked each by a median groove, the two grooves being the lines of inflection of a large endosternal structure ( $H$ , *Endst*). The sternum of the propodeum is a narrow, weakly sclerotized transverse band ( $F$ , *IS*) lying in the ventral membrane between the hind legs and the abdominal petiole. Laterally it connects with the lower margins of the propodeal tergum behind the legs.

According to a recent interpretation of the ventral sclerotization of the insect thorax by Ferris (1940), the apparent sternal areas of the mesothorax and the metathorax of the bee (fig. 16 F,  $S_2$ ,  $S_3$ ) would probably be regarded as ventral continuations of the pleura, the true sternal parts being supposed to be entirely folded in to make the base of the endosternum. The evidence presented in favor of this interpretation, however, is argumentative, and does not include a consideration of the dorsoventral muscles, which appear to be tergo-sternal in their attachments among generalized insects. It also seems to assume that morphological regions of a segment necessarily follow shifts in the sclerotization, rather than the converse, that sclerotized areas may expand or contract in a continuous and otherwise stationary integument. In the chalcidogastrous family Xyelidae, among the Hymenoptera, the episternal sclerotizations of the mesothorax are extended downward onto the ventral surface, where they are continuous across the median line in a narrow or wide bridge. Behind the bridge, however, is a large, triangular basisternal plate with a strong median groove, and on this sternal plate are attached the lower ends of the dorsoventral muscles. In most other Hymenoptera the

muscle-bearing areas of the ventral sclerotization are continuous with the episternal areas, as in the honey bee, but in some forms, as in the tenthredinoid *Arge*, the two are separated by distinct sutural lines.

*The pterothoracic endosternum.*—The sternal areas of the mesothorax and the metathorax support together a large endoskeletal structure similar to the endosternum of the prothorax, except that the sides are produced into *two* pairs of divergent arms (fig. 16 H, *Endst*) and the entire structure arises from the median inflections of the two sterna. The pterothoracic endosternum, therefore, appears to be composed of two ordinary Y-shaped sternal furcae united at their bases, which latter are stretched out anteriorly and posteriorly in the median ridges of the supporting sternal plates. The supra-neural bridge, however, spans the space between the bases of the anterior arms, and thus appears to belong to the mesothoracic component only. The long anterior, or mesothoracic, arms (*SA*<sub>2</sub>) extend laterally and upward to the sides of the thorax, where each arm ends in a thin, forward-curved expansion that gives attachment to a large group of short muscle fibers (79) arising on the posterior epimeral region and on the small pleural apophysis of the mesopleuron (fig. 17 G). The shorter posterior, or metathoracic, arms (fig. 16 H, *SA*<sub>3</sub>) go laterally and posteriorly over the bases of the second legs, just beyond which each arm unites solidly with a thick ridge (*o*) following the external suture (*m*) between the metapleuron and the propodeum (fig. 15 *m*). The pterothoracic endosternum gives attachment to the ventral intersegmental muscles between the prothorax and the mesothorax (fig. 22 C, 52, 58), and between the metathorax and the second abdominal segment (fig. 27 E, 118, 119), to muscles of the second and third legs (figs. 22 C, 24 A), to the muscles of the axillary levers of the mesothoracic wings, and to the tergosternal muscles of the metathorax (fig. 21 F, 97, 98, 99).

#### IV. THE WINGS

The movements of an insect's wings fall into two distinct categories: first, there are the movements of flight when the wings are extended, and second, the movements by which the wings are turned posteriorly over the body when at rest, or again brought into the extended position preliminary to flight. The action of the wing muscles that produce the movements of flight depends chiefly on structural adaptations in the skeletal parts of the thorax; the effect of the muscles concerned in the flexion and extension of the wings, on the other hand, is mainly dependent on structural details in the wing bases.



In other words, both sets of wing movements are produced by primitive muscles that have become motors of the wings by modifications in the skeletal elements, the primary changes that made flight possible being mostly in the thoracic skeleton, the secondary adaptations for flexion and extension being largely in the bases of the wings themselves.

In the bee the principal muscles of flight are the huge longitudinal and dorsoventral muscles of the mesothorax (fig. 16 C). For this

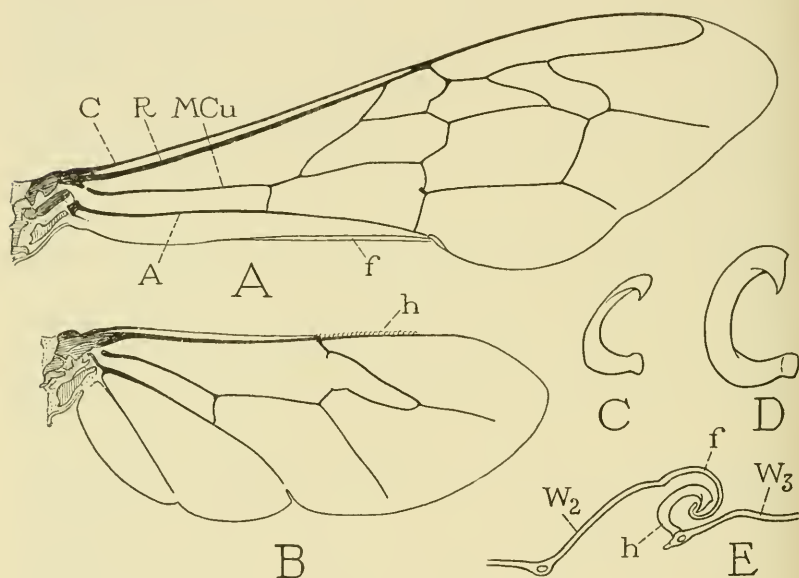


FIG. 18.—The wings.

A, B, fore and hind wing of drone. C, hook of hind wing of worker. D, hook of hind wing of drone. E, section of interlocked wing margins.

f, deflected fold on posterior margin of fore wing; h, hooks on anterior margin of hind wing.

reason probably the two wings on each side, when extended, are attached to each other. The coupling mechanism consists of a series of small hooks on the anterior margin of the hind wing (fig. 18 B, *h*) and a fold on the posterior margin of the fore wing (A, *f*). The hind-wing hooks, or *hamuli* (C, D), curve upward and backward from the marginal vein of the wing with a twist in the direction of the wing tip. The fold of the fore wing is a rounded deflection of the posterior part of the elevated wing area behind the last vein, and has a narrowly upturned margin (E, *f*). When the wings are extended preparatory to flight the fore wing is drawn over the upper



surface of the hind wing, and the hooks of the latter become engaged in the fold of the former (E).

*The fore wing.*—The mesothoracic wing of the bee is much larger than the hind wing (fig. 18) and has a stronger and more elaborate venation. The four veins that arise at the base of the wing are probably *costa* (A, C), *radius* (R), *media-cubitus* (MCu), and an anal, or vannal, vein (A). It is difficult to identify the branches of these main veins in the coarse reticulation of the distal part of the wing, but it will not be necessary for a study of the wing mechanism; an understanding of the basal structure of the wing, however, is of much importance.

The base of the fore wing is overlapped by a large scalelike lobe known as the *tegula* (figs. 15, 19 A, *Tg*), which is flexibly attached to the margin of the scutum just before the wing. In the wasp *Vespula* Duncan (1939) finds a small depressor muscle of the tegula arising on the scutum, but the writer has observed no muscle connected with the tegula in *Apis*.

In the naturally extended position of the fore wing, the wing base is rolled on itself (fig. 19 A), the posterior part being turned downward so that little of it is visible when viewed from above. If the basal region is artificially spread out flat (D) the posterior part is seen to be an extensive area widening toward its attachment on the body. The whole region of the wing base presents at first sight a confusion of small irregular parts, some of which are expansions of the wing veins and others independent sclerites in the basal wing membrane. A closer study, however, soon shows that there is an orderly arrangement of the parts and a mechanical interrelationship between them, which latter becomes more evident when the wing is moved.

The anterior part, or humeral area, of the wing base (fig. 19 D) is occupied by a large irregular sclerotization, here termed the *humeral complex* because it appears to include parts derived from the bases of the first three veins and also a remnant of the subcosta, which is suppressed in the distal part of the wing. The posterior part of the wing base, or *axillary area*, contains several discrete sclerites, which are the *first*, *second*, *third*, and *fourth axillaries* (*1Ax*, *2Ax*, *3Ax*, *4Ax*), and a prominent, transversely elongate *median plate* (*m*). All these sclerotizations are held in a basal wing membrane, bordered posteriorly by a corrugated marginal thickening known as the *axillary cord* (*AxC*), which is continuous on the one hand with the posterior margin of the wing, and on the other with the lateral extremity of the scutellum of the mesonotum (F, J, *AxC*).

The first axillary (fig. 19 E, *1Ax*) is an elongate sclerite with a large anterior head (*b*) turned laterally on a curved neck, posterior to which is a wide lateral projection (*f*) and a smaller articular lobe (*c*) on the mesal margin. The sclerite is attached to the side of the mesonotum in such a manner (J) that its neck rests on the anterior lobe (*p*) of the notal wing process (F), and its articular lobe is closely hinged to the posterior lobe (*q*) of the wing process, while the tapering posterior end rests and turns in a concave surface on the lateral margin (*r*) of the scutal area of the mesonotum (J. *sct*), where normally (D) it is concealed in a pocket of the wing membrane beneath the fourth axillary (*4Ax*). In the natural position of the extended wing (A) the first axillary (*1Ax*) stands almost vertical; in the flattened wing base (D) it is seen that its head abuts against the humeral complex, and the lateral projection underlaps the median plate (*m*). The first axillary is the *anterior hinge plate* of the wing.

The second axillary (fig. 19 E, *2Ax*) is a thick sclerite standing vertically in the wing base. Its exposed upper surface (*i*) appears as a small oval plate (D) lying in the notch between the head and the body of the first axillary. Ventrally the second axillary articulates by an anterior knob (E, B, *j*) with the wing process of the pleuron, and by a posterior arm (*k*) is associated with the subalar sclerite (B, *Sa*) on the upper edge of the pleuron. The second axillary is the *pivotal sclerite* of the wing base, since it is the only axillary sclerite that articulates with the pleuron and gives the wing a solid support from below. In the bee the second axillary has no direct connection with any of the wing veins, though in most insects it is connected with the base of the radius.

The third axillary (fig. 19 E, *3Ax*) is an elongate sclerite lying close along the axillary cord (D), with its tapering distal end associated with the enlarged base of the single anal vein of the wing. Proximally the third axillary bears a large lobe (E, *l*) projecting anterior to its axis, on which are inserted three muscles arising on the mesopleuron (H). The small, flat uppermost muscle (H, *76a*) arises in the pocket of the inner wall of the pleuron (fig. 17 B) beneath the reflected plate (*g*); the other two larger muscles (fig. 19 H, *76b*, *76c*) arise ventrally on the episternum. The third axillary is the only axillary sclerite of the wing base provided with muscles; it is the effective skeletal element of the wing-flexing mechanism, and may be termed the *flexor sclerite*.

The fourth axillary (fig. 19 E, *4Ax*) is a small, irregularly triangular sclerite lying transversely in the posterior angle of the wing base (D), articulated mesally on the lateral margin of the scutal area

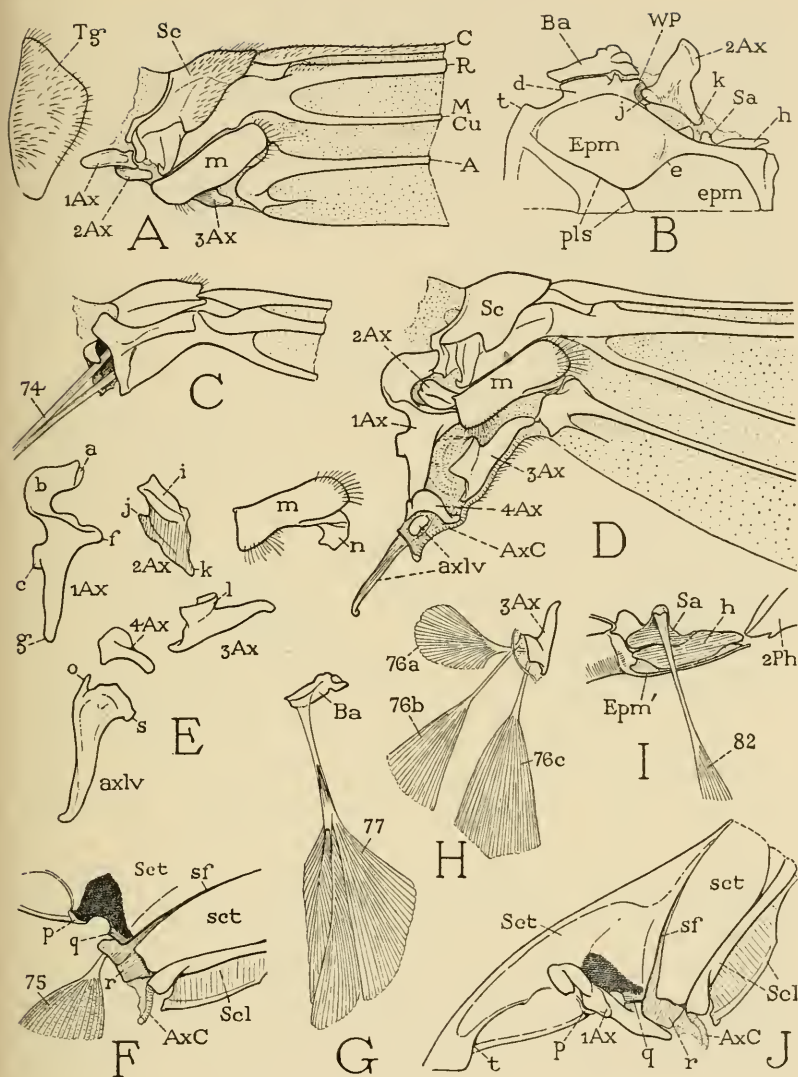


FIG. 19.—Details of the mesothoracic wing base, its articulations, and pleural muscles (drone).

A, tegula (Tg), and wing base in natural position of extended wing. B, upper part of mesopleuron, showing pleural articulation of basalare and second axillary. C, humeral area of wing base, ventral view. D, base of right wing with axillary region flattened, dorsal view. E, axillaries and axillary lever of right wing. F, left margin of mesonotum in region of wing attachment. G, right basalare and its muscle, mesal view. H, right third axillary and its muscles, mesal view. I, right subalare and its muscle, with supporting sclerite (h) on edge of epimeron, mesal view. J, left lateral part of mesonotum, with first axillary in natural position.

a, articular surface of first axillary with humeral complex of wing base; b, head of first axillary; c, notal hinge-lobe of first axillary; d, lobe of mesopleuron supporting basalare; e, recurrent suture of mesopleuron; f, lateral process of first axillary; g, posterior end of first axillary; h, supporting plate of subalare; i, exposed dorsal surface of second axillary; j, pleural articular process of second axillary; k, posterior ventral process of second axillary; l, muscle lobe of third axillary; m, median plate of wing base; n, distal lobe of median plate; o, articular process of axillary lever; p, anterior lobe of anterior notal wing process supporting neck of first axillary; q, posterior lobe of anterior notal wing process articulating with hinge-lobe of first axillary (c); r, posterior notal wing process; s, exposed head of axillary lever; t, point at which mesoscutum is supported on anterior angle of pleuron.

of the posterior plate of the mesonotum (F, J, *r*), above the posterior end of the first axillary (D). Its narrow outer end is closely pressed against the axillary cord not far behind the proximal end of the third axillary. The fourth axillary is the *posterior hinge plate* of the wing, but in the bees it has an accessory function in connection with the flexion of the wing by reason of its close association with a leverlike sclerite (D, *axlv*) lying immediately behind it and connected with the arm of the postphragma.

The axillary lever is an elongate triangular sclerite, as seen from the side (fig. 20 B), lying against the mesal surface of the stalk of the mesothoracic postphragma (A, *axlv*). By a small process (*o*) on the ventral angle of its base, directed anteriorly, the lever articulates with the narrowed extremity of the phragma stalk, and on its decurved distal end is attached a relatively large, fan-shaped muscle (78) arising ventrally on the mesothoracic arm of the pterothoracic endosternum. The sclerite is an internal structure except for the end of the thick dorsal angle of its base (*s*), which comes to the surface in the membrane of the posterior angle of the wing base, and appears here externally as a small sclerite lying immediately behind the fourth axillary (fig. 19 D, *axlv*). The function of the lever will be described in connection with the mechanism of the wing.

So far as yet observed the axillary lever is a free sclerite only in the Apoidea. In other Hymenoptera it is represented by an immovable arm or lobe of the postphragma, on which, however, there is always attached a muscle from the mesothoracic endosternum. In *Sphécus* (fig. 20 C) and *Vespula* (D), for example, the lever of *Apis* is so closely imitated by a long decurved arm (*t*) arising by its widened anterior end from the mesal surface of the stalk of the phragma that there can be no question of the homology of the two structures. In the ichneumonid *Megarhyssa lunator* (E) the corresponding arm (*t*) is simply a backwardly directed process of the phragma, and in the chalastogastrous genera *Sirex* (F), *Pteronidea* (G), and *Cimbex* (H) it is a mere process or lobe (*t*) of the lateral part of the phragma giving attachment to an endosternal muscle (78). In these last forms the muscles evidently pull downward on the phragma and probably depress the phragma-bearing postnotal plate ( $PN_2$ ). According to Duncan (1939) the muscle of the phragma arm in *Vespula* "resists the tendency of the indirect depressor muscle of the forewing (attached on the phragma) to lift the mesopostphragma, and helps to retract the phragma to the position of rest following a contraction of the indirect depressor muscle." The development of this structure into an accessory of the wing-flexing ap-



paratus in the bees is a highly interesting example of the evolution of a special mechanism from a structure having originally a quite different function.

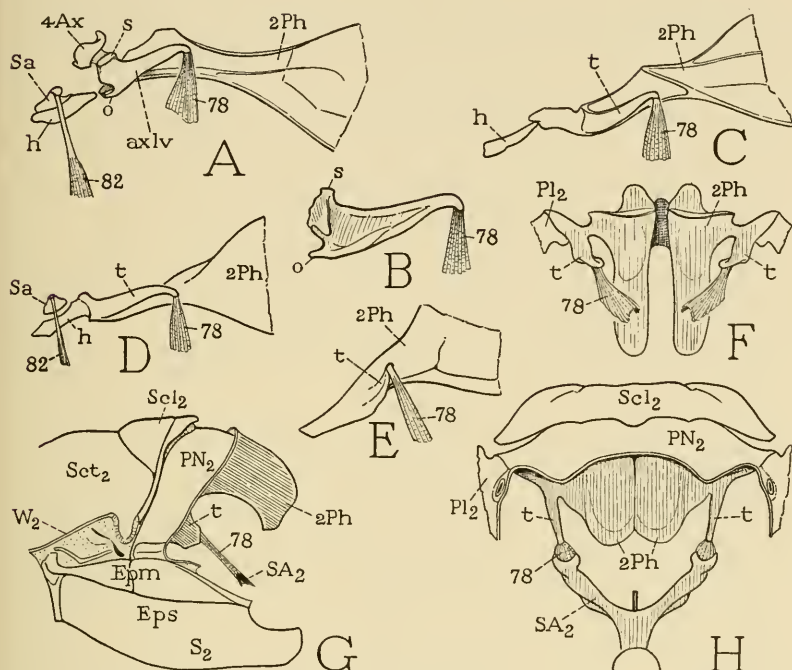


FIG. 20.—Evolution of the axillary lever.

A, *Apis mellifera* L., drone, right stalk of second phragma, mesal view, showing axillary lever (*axlv*) and associated fourth axillary of wing base. B, same, left axillary lever, lateral view. C, *Sphecius speciosus* (Drury), right stalk of second phragma with mesal process (*t*) corresponding with axillary lever of *Apis*. D, *Vespula maculata* (L.), same parts as in *Sphecius* (C). E, *Megarhyssa lunator* (F.), right stalk of phragma with simple muscle process, mesal view. F, *Sirex abbottii* Kirby, second phragma and lateral muscle lobes (*t*), anterior (ventral) view. G, *Pteronidea ribesii* (Scop.), mesothorax and second phragma, lateral view, showing muscle lobe (*t*) with muscle from furcal arm (*SA*<sub>2</sub>). H, *Cimbex americana* Leach, posterior end of mesonotum with second phragma, showing lateral muscle processes (*t*) connected by short muscles (*78*) with arms of mesosternal furca.

*h*, supporting sclerite of subalare; *o*, articular process of axillary lever; *s*, exposed head of axillary lever associated with fourth axillary sclerite; *t*, muscle-bearing process of second phragma of non-apoid Hymenoptera corresponding with axillary lever (*axlv*) of Apoidea.

The large, transversely elongate median plate in the base of the fore wing (fig. 19 E, *m*) lies close behind the humeral complex (A, D), and forms a link between the first and second axillaries at its mesal end, and the enlarged base of the fourth wing vein at its



distal end. In most insects the median plate is associated with the bases of the veins media and cubitus, but in the Hymenoptera these two veins appear to be combined, and united basally with the radius.

*The hind wing.*—The small metathoracic wing of the bee (fig. 18 B) has a more simplified venation than the fore wing, but it has the same vein stems in its proximal part (fig. 21 A) except that there are two veins (1A, 2A) in the vannal region. The basal structure of the hind wing also is simpler than that of the fore wing, and there is no metathoracic tegula. The humeral complex supports only the first two veins; a median plate and a fourth axillary are absent.

The relatively small first axillary of the hind wing (fig. 21 A, B, 1Ax) articulates on the lateral plates of the metanotum (E), its posterior process being received in a depression (f) of the lower angle of the semi-detached plate ( $n_3$ ), its head resting on a small lobe (e) of the free plate (d). Laterally the large head of the first axillary abuts against the broad mesal end of the humeral complex (A). The irregular second axillary (B, 2Ax) lies laterad of the first axillary (A) and articulates by a large ventral process in a notch on the dorsal margin of the metapleuron (C). The third axillary is a large, elongate sclerite (B, 3Ax) lying obliquely transverse behind the second axillary (A) between the edge of the metanotum and the base of the fourth wing vein. The large, fan-shaped, three-branched muscle of the wing-flexing third axillary (B, F, G, H, 100) arises on the anterior infold of the metapleuron (C, H, k) and is attached, not directly on the third axillary, but on a minute sclerite of the wing membrane (A, B, a) close to the base of the axillary, and hence pulls indirectly on the latter through the intervening membrane.

*The epipleurites.*—The epipleural sclerites associated with the under sides of the wing bases include in each segment the *basalare* lying before the pivotal second axillary, and the *subalare* lying behind it. The sclerites are articulated on the upper edges of the pleura; they give insertion to muscles that deflect them inwardly and thus pull on the wing bases by reason of the close membranous connection of the epipleurites with the latter. The specific effect of the epipleurite muscles on the wing movements will be described later.

The *basalare* of the mesothorax (fig. 19 B, Ba) is an elongate sclerite hinged by its entire length on a wide lobe (d) of the dorsal margin of the mesopleuron, which supports posteriorly also the second axillary (2Ax). On the inner surface of the *basalare* is attached by a strong apodemal tendon a large, flat, fan-shaped muscle (G, 77) arising on the anterior part of the pleuron (fig. 17 E), where it partly overlaps internally the second and third muscles of the third

axillary (76*b*, 76*c*). The contraction of this muscle turns the basalar inward on the supporting pleural lobe, and the movement is transmitted to the wing because of the close connection of the basalar with the humeral angle of the wing base.

The subalar of the mesothorax is a small triangular sclerite (fig. 19 I, *Sa*) but little visible in lateral view (B) beneath the posterior part of the wing. Its broad base is supported on a longer sclerite (I, *h*), which in turn rests on the inner margin of the inflected dorsal plate of the epimeron (*Epm'*), and is linked posteriorly with the anterior extremity of the stalk of the postphragma (*zPh*). On the upper angle of the subalar is attached the tendon of a long muscle (82), which arises ventrally on the mesothoracic coxa (figs. 17 G, 22 C, 82). The subalar is closely associated with the posterior basal process of the second axillary sclerite (fig. 19 B), so that the pull of its muscle is indirectly transmitted to the pivotal sclerite of the wing base.

The epipleural sclerites of the metathorax have the same relations to the hind wing as do those of the mesothorax to the fore wing. The triangular basalar (fig. 21 B, *Ba*) sits on a marginal elevation of the metapleuron before the second axillary (C, *Ba*), and the small subalar (B, *Sa*) is attached to the concave pleural margin behind the second axillary (C, *Sa*). A single large basalar muscle (H, 101) arises on a lobe (*r*) of the ridge in the metapleural area behind the middle leg (fig. 16 H, *r*), and tapers upward to a strong tendon attached mesally on the basalar sclerite (fig. 21 B, H, *Ba*). The small, inconspicuous subalar (B, *Sa*) has an elongate apodemal process on which are inserted two muscles, one a long fusiform muscle (105), corresponding with the subalar muscle of the mesothorax, which arises ventrally on the hind coxa (fig. 24 A, 105), the other a broad thick muscle (fig. 21 B, C, H, 102) arising on the upper plate of the metapleuron, and apparently represented in the mesothorax by a similar pleural muscle (fig. 17 E, 75) attached dorsally on the margin of the posterior scutal plate of the mesonotum (fig. 19 F, 75). The subalar is intimately associated with the second axillary of the wing base (fig. 21 B, 2*Ax*) by a close membranous connection (*b*) with the posterior basal arm of the latter.

*The mechanism of flight.*—To understand the movements of an insect's wings it is necessary to observe first that the wings are supported from below on the second axillary sclerites of their bases, and that these sclerites rest on the upper edges of the pleura, while the flexible attachments of the wings to the notal plates lie a little mesad of the pleural supports. As a consequence a slight depression of the

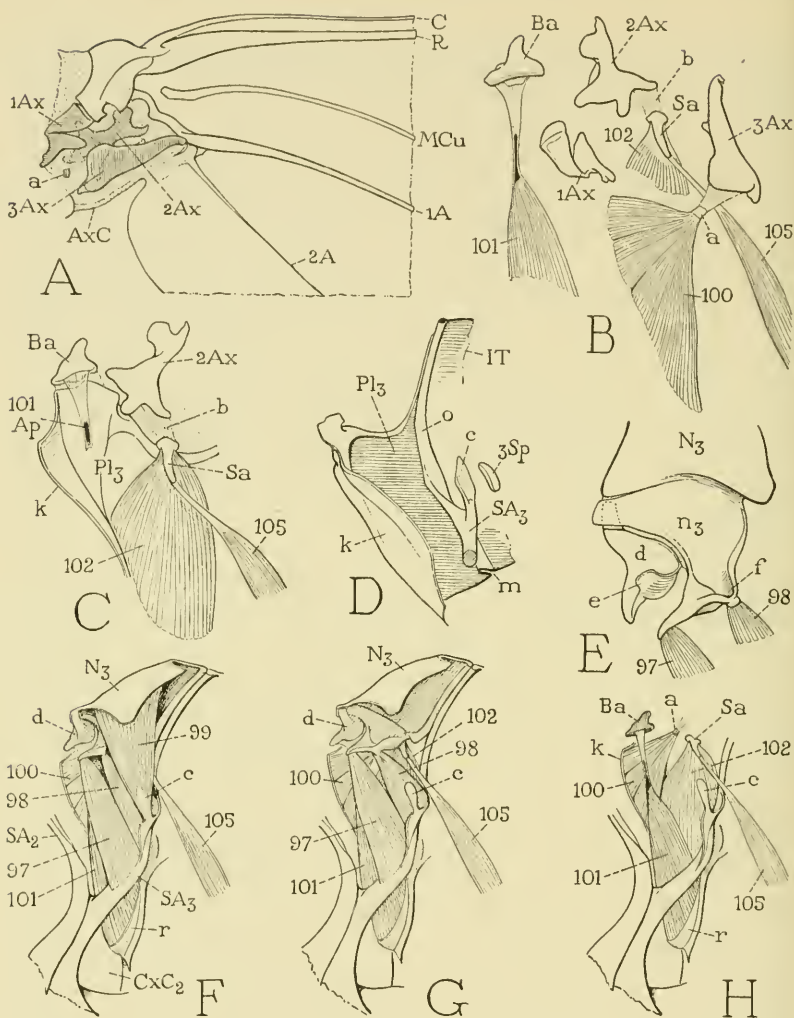


FIG. 21.—Details of the metathorax, base of the hind wing, and the lateral metathoracic muscles (drone).

A, base of hind wing, dorsal view. B, axillary, basalar, and subalar sclerites of hind wing, dorsal view. C, inner face of upper part of right metapleuron, showing pleural articulations of basalar, second axillary, and subalar, and muscles of subalar. D, upper part of right metapleuron and adjoining part of propodeum, anteromesal view. E, lateral part of metanotum, left side. F, lateral muscles of metathorax, right side, mesal view. G, same, with third tergosternal muscle (99) removed. H, same, with notum and first, second, and third tergosternal muscles (97, 98, 99) removed, exposing basalar and subalar muscles (101, 102, 105) and muscle of third axillary (100).

a, nodule of wing membrane giving insertion to muscle of third axillary; b, "ligament" of wing membrane connecting second axillary with subalar; c, process of metathoracic endosternal arm ( $SA_3$ ) giving attachment to third tergosternal muscle (99); d, free marginal sclerite of metanotum; e, lobe of d supporting head of first axillary; f, posterior articular socket of first axillary; k, anterior inflection of metapleuron; m, groove between metapleuron and propodeum; n<sub>3</sub>, semidetached lateral plate of metanotum; o, internal ridge between metapleuron and propodeum, r, lobe giving attachment to basalar muscle (101).

lateral margins of the back plates of the wing-bearing segments causes the wings, in the *manner* of a pump handle, but involving the interaction of many structural details, to turn upward, and an elevation of the notal margins tilts the wings downward. The up-and-down movements produced in this way, however, are not sufficient for progressive flight; in addition the wings must have a partial rotary movement on their long axes accompanied by a forward and rearward motion, by which the anterior margins are turned downward and forward during the downstroke, and reversed during the upstroke. This compound motion gives a sculling movement to each wing, but the result of the wings on opposite sides of the body acting together is that a current of air is driven backward, and the insect propelled forward. In the bee the two wings of each side act in unison as a single pair of flight organs because of their connection with each other, but the unity of action is further secured by a reduction of the metathoracic musculature and its subordination to the action of the highly developed mesothoracic muscles, which latter thus become the chief motor elements for both pairs of wings.

The cavity of the pterothorax is largely occupied by the huge dorso-ventral and dorsal longitudinal muscles of the mesothorax (fig. 16 A, C). The thick pillars of dorsoventral muscles (72) have their upper attachments (A) on the lateral parts of the anterior plate of the mesonotum (B), and go downward and backward (C) to their lower attachments on the ventral and lower lateral walls of the pleurosternal region of the mesothorax. The longitudinal muscles (71) are attached anteriorly on the prephragma and the median area of the anterior notal plate (B), and extend posteriorly through the metathorax into the posterior end of the propodeum, where they are attached on the postphragma (2Ph). Though the postphragma of the bee is extended through the metathorax far back into the propodeum, to accommodate the great length of the mesothoracic dorsal muscles, it is morphologically an ingrowth between the mesonotum and the metanotum. A pair of small fan-shaped muscles (C, 96), arising on a median process of the posterior end of the propodeal tergum (IT) and spreading to their insertions on the rear surface of the phragma, must represent, therefore, the usual longitudinal dorsal muscles of the metathorax with their posterior attachments transposed backward on the propodeum. A pair of short external dorsal muscles of the mesothorax (D, 70) traverses the scutellar area of the mesonotum.

The vertical component of the upstroke of the fore wings, resulting from a depression of the lateral margins of the mesonotum, is effected principally by the great dorsoventral muscles (fig. 16 C, 72), but



probably important adjuncts are the large pleuronotal muscles arising on the sides of the pleuron (fig. 17 E, 75) and attached on the ends of the posterior scutal areas of the notum (fig. 19 F, 75). The wing bases, hinged to the back by the first and fourth axillary sclerites, are pressed downward proximal to the fulcral second axillaries by the descending margins of the notum, and thereby the distal parts of the wings are thrown upward. The vertical component of the downstroke, conversely, results from the contraction of the longitudinal muscles, which restores and increases the curvature of the mesonotum, and thus turns the wings down on the fulcral sclerites.

In most insects the wing-bearing plates of the back are sufficiently thin and flexible to respond by changes in shape to the alternating pull of the vertical and longitudinal muscles. Such movements, however, are not possible in the thick and rigid mesonotum of the bee and related Hymenoptera, and it is for this reason that the mesonotum is cut by a transverse fissure (fig. 16 C, *sf*) into an anterior and a posterior plate. The fissure widens on each side into an open cleft (fig. 19 J, *sf*), the edges of which are connected by an infolded membrane. The closed dorsal part of the fissure acts as a hinge between the two plates. Pressure on the top of the back depresses the notal plates at the hinge line and widely opens the lateral clefts, the anterior notal plate here moving forward, the posterior plate backward. The divergent movement of the two plates, however, accentuates the downward movement of their lower margins at the points just before and behind the lateral clefts where the wings are articulated to the back by the first and fourth axillary sclerites. This action of the mesonotum is easily demonstrated by manipulation of a dead bee, and could be well illustrated with half of a hollow rubber ball having a meridional slit on each side.

In the chalastogastrous Hymenoptera the posterolateral areas of the mesoscutum form deep concavities of the scutal surface at the sides of the elevated median area of the scutellum, and are separated from the main part of the scutal plate before them by the lines of abrupt deflections of the notal surface. These lines coincide with the scutal clefts of the Clistogastra, and, in fact, each is split laterally by a short cleft. The response of the relatively flat mesonotum of a tenthredinid to gentle compression between its two ends is most pronounced on the sides; the anterior wing processes spread laterally and move upward and posteriorly, the lateroposterior margins of the anterior scutal areas at the lateral clefts folding backward above the anterior edges of the posterolateral areas. In the densely sclerotic and strongly convex mesonotum of the Clistogastra a much deeper splitting



of the scutum has become necessary for carrying out the mechanical function of the notum. The scutal clefts of the Hymenoptera in any case, are simply extensions of the usual lateral emarginations of a wing-bearing notum that are bridged by the first axillary sclerites of the wing bases.

The opening of the scutal clefts by pressure on the back causes a posterior displacement of the postphragma in the propodeum because of the connection of the phragma with the scutellum (fig. 16 C), and this movement of the phragma must stretch the longitudinal muscles preparatory to their succeeding contraction. The contraction of the longitudinal muscles (71), extending from the anterior notal plate to the phragma, not only closes the lateral clefts of the notum, but causes the edges of the posterior plate to slide beneath those of the anterior plate, thus increasing the curvature of the back to give greater effectiveness to the downstroke of the wings. The small propodeal muscles (96) attached on the back of the phragma may be supposed to contribute to the movement of the phragma, though their narrowed and convergent posterior ends (fig. 27 C, 96) would suggest that they pull on the propodeum. The function of the pair of delicate muscles in the mesothoracic scutellum (fig. 16 D, 70) is not clear.

The metathorax contains no muscles corresponding in function with the dorsal muscles of the mesothorax, since the only intersegmental dorsal muscles that can be referred to the metathorax are the greatly displaced pair between the postphragma and the propodeum (fig. 16 C, 96). The dorsal muscles of the mesothorax (71), therefore, must cause the downstroke of both pairs of wings when the wings of each side are connected. Probably in the same way the dorsoventral muscles of the mesothorax are largely responsible for the upstroke of the metathoracic wings, since as long as the wings are connected pressure on the mesonotum alone lifts both pairs of wings, though it has no effect on the hind wings when the latter are unhooked. However, the metanotum itself is amply provided with depressor muscles, which very probably in the living bee play an important part in the elevation of the wings.

In each side of the metathorax there are three large muscles attached on the notum, which arise ventrally on the metathoracic arm of the pterothoracic endosternum. The first two of these muscles (fig. 21 F, G, 97, 98) arise by broad bases on the endosternal arm and taper upward to their dorsal attachments on the lower edge of the semidetached lateral plate of the notum (E,  $n_3$ ). The third and largest muscle (F, 99) arises from a small lobe (c) of the endosternal arm, and its fibers spread upward to their attachments on the lateral

triangular area of the dorsal part of the notum. A downward pressure on this region of the metanotum at once turns the hind wings upward, leaving little doubt that the metanotal muscles are wing elevators.

The horizontal and rotary components of the wing motion, by which the wings are turned forward with the costal margins deflected during the downstroke, and reversed during the upstroke, are produced chiefly by the muscles of the basalar and subalar sclerites. It is these movements that convert the wings from mere flaps into organs of propulsion. The mechanism involved is equally developed in each wing-bearing segment of the bee. The epipleural sclerites, as already explained (figs. 19 B, I, 21 C, *Ba*, *Sa*), are hinged to the upper edges of the pleura in such a manner that the contraction of their muscles turns them mesally in the subalar membranes. The movements of the sclerites are effective on specific points in the wing bases because a tract of the membrane intervening between each sclerite and the wing is so tightly stretched that it acts as a direct union, and often gives a superficial appearance of being a connecting ligament. The basalar in each wing of the bee is thus connected with the humeral complex of the wing base, and the subalar with the posterior lever arm of the second axillary (fig. 21 B). Contraction of the basalar muscle during the downstroke of the wing, therefore, revolves the basalar inward on its pleural hinge, and the tension exerted on the wing base turns the descending wing forward on the pivotal second axillary and deflects its costal margin. Similarly, during the upstroke, the subalar muscle acting on the subalar pulls on the lever arm of the second axillary and thus tilts the wing downward posteriorly, so that the costal margin turns upward and moves backward, relative to the body, while the wing is ascending.

*Flexion and extension of the wings.*—When the bee alights after flight, or when the organs of flight are not otherwise in use, as in “fanning,” the wings are flexed posteriorly, the hooks on the hind wings automatically loosing their grasp on the fore wings, and both pairs of wings are laid over the back, the fore wings on top of the hind wings. The mechanical problem involved in the horizontal flexing of an insect’s wing may be illustrated with a piece of paper firmly held flat at one end and bent horizontally on itself; the bending necessarily produces a fold across the base. Conversely, if the paper is folded in the same way, it automatically bends backward at a right angle to its flat position. The flexing apparatus of the wing acts on the second principle—by the *production* of a basal fold the wing is turned horizontally backward. The fold-producing mechanism is the

third axillary sclerite and its muscles, but in the fore wing of the bee the action of the third axillary appears to be assisted by the fourth axillary and its lever.

The basal region of the fore wing of the bee in the natural position of extension (fig. 19 A) is rolled on itself in such a way that most of the axillary area is deflected. There is hence an oblique fold in the wing base extending from the head of the first axillary (*1Ax*), behind the second axillary and the median plate, to the upwardly directed distal end of the third axillary (*3Ax*). The pull of the third axillary muscles (H), therefore, simply revolves the sclerite mesally and somewhat forward on its base and thus accentuates the fold already present, with the result that the distal part of the wing turns backward. If the wing base were flat (D), as it is in most insects, the action would not be essentially different, as can be demonstrated by revolving the third axillary in the wing of a dead specimen.

The part that the fourth axillary plays in the flexing of the fore wing of the bees can be shown by depressing its lever (fig. 19 D, *axlv*). The fourth axillary (*4Ax*) is movably articulated on the margin of the mesonotum and its distal end is pressed against the axillary cord (*AxC*). The head of the lever lies in the wing membrane immediately behind the fourth axillary. A downward pull on the lever muscle (fig. 20 A, *78*) depresses the lever on its fulcral connection (*o*) with the end of the postphragma, and causes the head (*s*) to pull backward on the fourth axillary (*4Ax*). The axillary turns on its notal articulation and its outer end pulls on the axillary cord. The wing gives a quick response with a slight backward movement. Slight though this movement of the wing is, the elaborateness of the mechanism that produces it suggests that the movement is one of considerable importance. It may be seen, in fact, that the backward jerk on the extended wing brings the third axillary into a more nearly vertical position in which it becomes quickly responsive to the action of its own muscles. The fourth axillary and its lever in the fore wing of the bee, therefore, appear to be a starting apparatus for the flexor mechanism.

The flexing of the hind wing is produced entirely by the large third axillary sclerite and its muscle (fig. 21 A, B, *3Ax*), since there is no fourth axillary or lever accessory. The axillary region of the hind wing, however, unlike that of the fore wing, is approximately flat when the wing is extended (A). It is probable, therefore, that on relaxation of the extensor muscle the wing automatically turns backward sufficiently to raise the third axillary into a position in which its muscle can become effective.

The extension of the flexed wings preparatory to flight is in general produced by the basalar sclerites and their muscles. In a dead specimen a slight pressure on the basalare of either wing, or a pull on its muscle, brings the wing out at right angles to the body and deflects its anterior margin. The fore wing of the bee, however, is provided with a small pleuroalar muscle (fig. 19 C, 74), which arises on the anterior marginal carina of the mesopleuron (fig. 17 C, 74) just below the attachment of the spiracular muscle (73), and extends dorsally and posteriorly to its insertion by two branches attached ventrally on the humeral complex of the wing base (fig. 19 C). This muscle evidently must be an accessory wing-extensor. In some insects a depression of the second axillary, produced by the pull of the subalar muscle, helps to extend the wing, but an extensor action of the second axillary cannot be demonstrated in the bee.

## V. THE LEGS

The legs of Hymenoptera have the usual six segments of an insect leg, namely a *coxa*, a *trochanter*, a *femur*, a *tibia*, a *tarsus*, and a *pretarsus*. A *leg segment* is to be defined as a section of the limb independently movable by muscles attached on its base, except where there is evidence of the union of segments or a suppression of muscles. The tarsus is usually divided into subsegments, or *tarsomeres*, which, though movable on each other, are not "tarsal segments" since only the proximal piece is provided with muscles. The flexible areas between segments or subsegments are the *joints* of the leg. The proximal tarsomere, especially when differentiated by size or other features, as in the bee, is designated the *basitarsus*. The pretarsus either terminates in a single claw, or *dactyl*, or it bears a pair of lateral claws, or *ungues*, and usually a median lobe, the *arolium*.

The three pairs of legs of the bee are attached at somewhat different angles on the thorax so that in their action they are radially distributed at the sides of the body. The coxae of the fore legs hang downward on transverse axes of movement (fig. 11 G, *Cx*), and hence the first legs swing forward and backward in the transverse planes of the coxae. The middle coxae are transversely elongate and set obliquely into the under wall of the thorax (figs. 15, 16 F), and the trochanters are attached at their mesal ends; the middle legs, therefore, are limited in their up-and-down motion, and swing forward and backward by the revolution of the coxae on the body. The hind coxae also have obliquely transverse axes on the thorax (figs. 15, 16 F), but they are directed posteriorly and hence give the hind legs a more



backward position at the sides of the abdomen. Each leg has characteristic features, and, in the worker particularly, various parts of the legs are developed into specific structures for special uses.

For descriptive purposes it is customary to name the leg surfaces according to the positions they assume when the limb is extended straight out from the body. In such a position the upper surface is *dorsal*, the under surface *ventral*, the preaxial surface *anterior*, and the postaxial surface *posterior*. The actual directions of the leg surfaces in normal positions, however, may be quite different.

Inasmuch as the legs differ principally in relative size, form, and outer structure, the general external features will be described separately for each pair, while the mechanism of the joints, and the muscles, which are but little different in the three pairs of appendages, will be treated collectively in order to avoid unnecessary repetition.

*The fore legs.*—The fore legs (fig. 13 A) are smaller than the others and have somewhat less freedom of motion because of the vertical position of the coxae (fig. 11 G), but, in compensation, the femur of each fore leg has an anterior twist (fig. 14 A) by which the tibia acquires a forward movement, and, when fully flexed, lies against the anterior surface of the femur and trochanter. The long, cylindrical, bristly first tarsomere is used as a brush for removing pollen or other particles from the head and fore parts of the body, but the most important special features of the first leg is the *antenna cleaner* at the base of the tarsus.

The antenna cleaner (fig. 14 B) consists of a deep semicircular notch (*b*) on the inner (ventral) face of the proximal end of the basitarsus (*Btar*), and of a large flattened spur (*a*) that serves as a clasp, or *fibula*, projecting from the inner angle of the distal end of the tibia (*Tb*). The posterior margin of the notch bears a comblike fringe, or *pecten*, of fine, closely set, spinelike hairs. The fibula is a broad, thin, movable appendage with a narrowed base, a tapering distal point, and a strong, spatulate accessory lobe (*e*) on its anterior surface. When the tarsus is flexed by the depressor muscle (E, 68) the proximal lobe of the basitarsal notch (C, *c*) glides under the accessory lobe (*e*) of the fibula, and the distal point of the tarsal notch (*d*) is caught in the angle between the two fibular lobes. The tarsal notch is thus closed to a semicircular aperture by the accessory lobe (*e*) of the fibula, and the larger flat lobe (*a*) overlaps the aperture posteriorly. When the organ is used by the bee, the tarsal notch is placed around the base of the antennal flagellum by movements of the leg, and then, by flexion of the tarsus, the antenna is pressed against the accessory lobe of the fibula, which latter resists the



pressure because of a small process of the tibia (*f*) that abuts against its base. The antenna is thus held securely and is now drawn upward through the cleaner, the tarsal comb brushing its sensory outer surface, the thin lobe of the fibula scraping its inner surface.

The antenna cleaner is not a gadget peculiar to the bees; it is developed in some measure in most of the clistogastrous Hymenoptera (fig. 14, F, G, H, I), though the tarsal notch is usually shallower than in the honey bee, and may be but a sinuosity of the tarsal margin. The fibula of the cleaner is simply a special development of an ordinary movable spur usually present on the end of the tibia, such as is present on the middle leg of the adult bee (fig. 22 A, B), and also on the hind leg of the pupa.

*The middle legs.*—The second legs are the least specialized of the legs in the bee, and have the simplest form in the drone (fig. 22 A). In each caste the end of the tibia is armed ventrally with a long spine, which has been said to be used by the worker for removing wax from the wax pockets of the abdomen, but the evidence of such use of the spine has been questioned. The basal tarsomere is long and cylindrical in the drone (A), in the worker and queen it is wide and flattened, in the worker (B) its under surface is thickly covered with long stiff hairs projecting distally, and serves as a pollen brush.

*The hind legs.*—The large hind legs are the most specialized in form of all the legs by reason of the great size and lateral flattening of the tibia and basitarsus (fig. 23 A, F, H). Though this feature is common to the three castes, a functional reason for it is not evident except as it is elaborated for useful purposes in the worker. The femur has a coating of small hairs in the drone (F), in the queen and the worker (A) it is bushy with long feathery hairs. The tibia of the drone (F), aside from its size and shape, has no special characters; in the queen (H) the tibia is relatively wider and thick at its base; in the worker (A) it is narrowed proximally and expanded distally, and its smooth, somewhat concave outer (anterior) surface (C) is bordered with long curved hairs, forming the pollen-carrying basket, or *corbicula*. The basitarsus is equally large in each caste (A, F, H), but there is no apparent reason for its size and shape in the queen and the drone; the cavity of the basitarsus is traversed by the tendon of the pretarsal claws and is otherwise occupied only by a loose mass of fat tissue. In the worker the inner (posterior) surface of the basitarsus (A, *Btar*) is armed with about 10 transverse rows of long, slender spines directed mesally and distally at an angle of 45°. The basitarsus of the worker thus resembles a flat brush or currycomb, and has been termed the *strigilis* (Betts, 1923), though the same

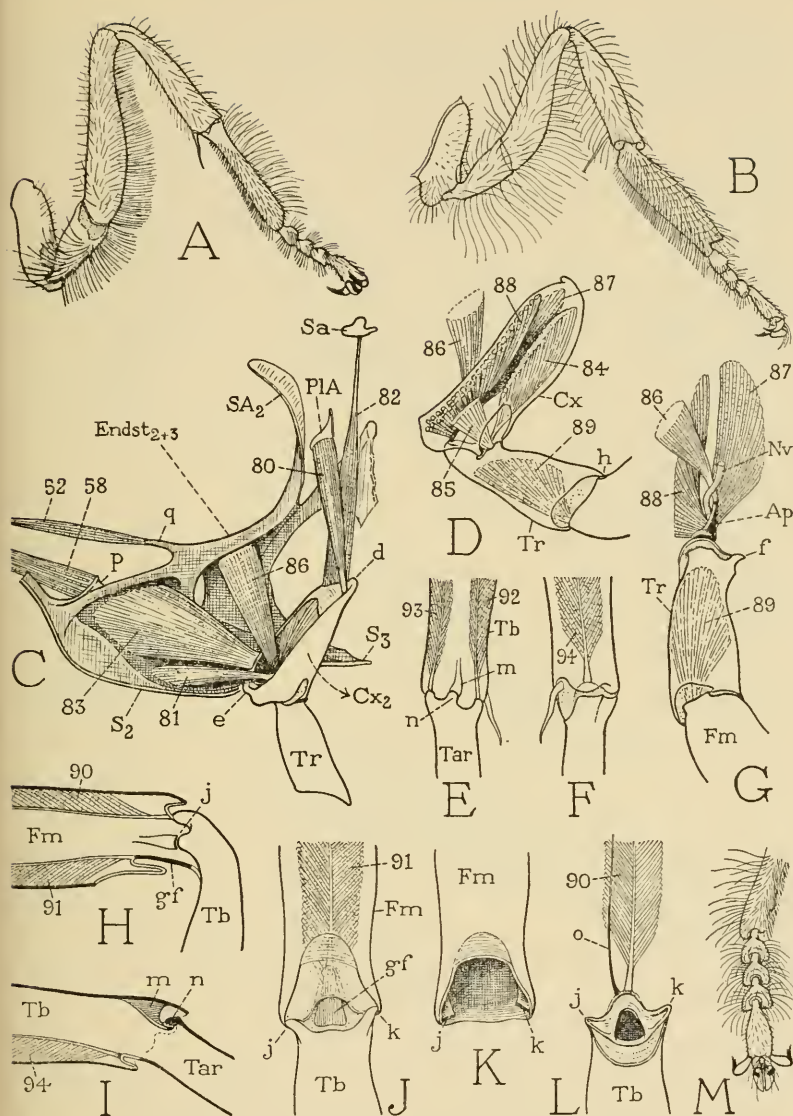


FIG. 22.—The mesothoracic leg and its muscles.

A, right middle leg of drone, posterior view. B, same of worker, posterior view. C, endosternum of pterothorax and mesothoracic coxa, with thoracic muscles of leg, left side (coxa turned outward). D, base of right middle leg of drone, posterior view, showing trochanteral and femoral muscles. E, tibio-tarsal joint of right middle leg of drone, dorsal view. F, same, ventral view. G, trochanter and base of femur of left middle leg of drone, with muscles, mesal view. H, diagram of dicondylar femoro-tibial joint. I, diagram of monocondylar tibio-tarsal joint (lateral muscles not shown). J, femoro-tibial joint of right middle leg of drone, ventral view. K, end of femur with tibia removed, ventral view. L, base of tibia, ventral view, showing levator muscle (90) and chordotonal ligament (o). M, tarsus and pretarsus of right middle leg of drone, dorsal view.

d, pleural articulation of coxa; e, sternal articulation of coxa; f, anterior coxal articular process of trochanter; h, dorsal articulation of trochantero-femoral joint; j, anterior femoro-tibial articulation; k, posterior femoro-tibial articulation; m, tibial articular process of tibio-tarsal joint; n, tarsal articular knob of tibio-tarsal joint; o, tendon of femoral chordotonal organ; p, process of endosternum giving attachment to muscle 58; q, process of supraeneural bridge of endosternum giving attachment to muscle 52.

name has been used for the antenna cleaner; the brush serves for the collection and retention of pollen to be stored in the pollen basket of the tibia. The deep notch in the dorsal margin of the hind leg between the tibia and the basitarsus is converted in the worker into a *pollen press* for the transfer of pollen from the basitarsal brush of one leg into the tibial basket of the other.

The pollen press of the worker bee is a simple adaptation of the pincerlike tibio-tarsal notch for pushing pollen from one side of the leg to the other and for compressing it in the pollen basket. The proximal end-surface of the basitarsus opposed to the distal end of the tibia (fig. 23 B) is beveled outward and upward toward the tibia and is expanded in a small lobe, known as the *auricle* (*au*), bordered by a fringe of long hairs. The surface of the auricle is covered with small spicules, and is limited mesally by a strong ridge. The opposing free end of the tibia bears mesally a row of short, closely set, sinuous spines, forming a little rake, or *rastellum* (*ras*), which projects down over the base of the auricle (D, E). Laterad of the rastellum the end-surface of the tibia is concave and is separated by a low ridge from the floor of the pollen basket above it on the outer (anterior) surface of the tibia (C, *cbl*). When the basitarsus is bent upward at the tibio-tarsal joint (D, E), the fringed lip of the auricle, guarded mesally by the rastellum, passes within the semicircle of long curved hairs on the lower end of the tibia and overlaps the floor of the pollen basket. As this gadget is used by the bee for loading the pollen basket, a small mass of pollen is first raked off from the basitarsal brush of the opposite leg by the rastellum of the tibia; the detached pollen falls on the rough surface of the auricle and adheres to it. Then, by an upward flexure of the tarsus on the tibia, the mass of pollen on the auricle, held in place by the rastellum, is pressed up into the tibial basket. With repeated scrapings and operations of the press the basket is finally loaded by successive increments of pollen added at the bottom of the mass.

It is interesting to note that both the antenna cleaner and the pollen press are developed at the tibio-tarsal joint. This joint differs from the other leg joints in that the tarsus has a monocondylic hinge on the tibia, and three muscles. Since this structure pertains to the corresponding joint in all the legs of the three castes of the bee, it is clear that it is not an adaptation to either the antenna cleaner or the pollen press. On the other hand, it is possible that the development of these instruments has depended on the peculiar nature of the tibio-tarsal joint and the unusual mobility of the tarsus.

*The coxae and their muscles.*—The movements of an insect's leg as a whole depend on the nature of the coxal articulation with the body. In the bee the coxae of all the legs swing forward and backward on

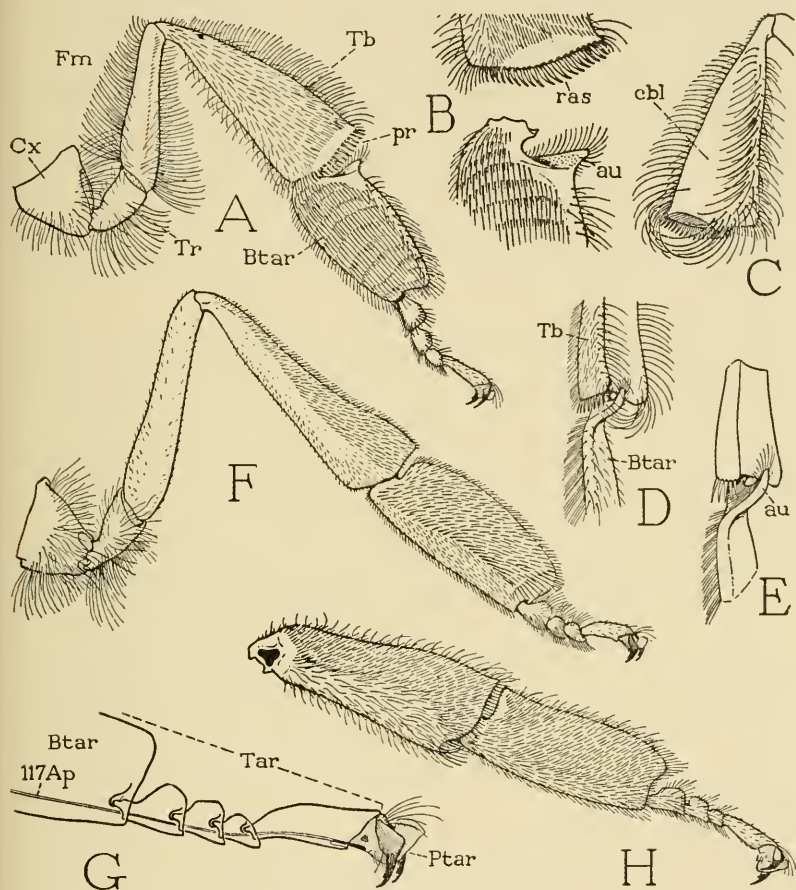


FIG. 23.—The metathoracic leg, external structure.

A, right hind leg of worker, posterior (inner) surface. B, opposing ends of tibia and basitarsus of right hind leg of worker, posterior view. C, anterior (outer) face of hind tibia of worker. D, pollen press of worker between tibia and basitarsus, dorsal view. E, same, better shown by removal of tibial hairs. F, right hind leg of drone, posterior (inner) surface. G, right hind tarsus and pretarsus of drone, posterior view. H, right hind tibia, tarsus, and pretarsus of queen, posterior surface.

transverse axes, and the muscles of each coxa are inserted anterior and posterior to the coxal axis of movement. The coxal muscles, therefore, are *promoters* and *remoters*. Morison (1927) designates



the coxal muscles "extensors" and "flexors," the "extensors" being the lateral muscles, the "flexors" the mesal muscles, but this nomenclature ignores the relation of the muscles to the natural movements of the coxae. Morison adds, however, that a further study "would doubtlessly result in a better nomenclature" for the muscles and a "more accurate statement of their functions."

The fore coxae are attached by articular membranes to the pleurosternal suspensorium of the prothorax with somewhat obliquely transverse axes between weak pleural articulations and the furcasternum (fig. 11 G); sternal articulations are absent, but the mesal angles of the coxae overlap the furcasternal margins. Though the fore coxae are thus freely suspended, their principal movements are forward and backward.

Each fore coxa has six muscles (fig. 13 C, D), two of which are promoters, three remoters, and one an intersegmental retractor of the propectus. Of the promoters, one (53) arises on the episternum and is inserted laterally on the anterior margin of the coxa, the other (54) takes its origin on the side of the prothoracic endosternum and is inserted mesally on the anterior coxal margin. The remoters include two lateral muscles and one mesal muscle. The first lateral remotor is a long muscle (C, D, G, 55) arising on the side of the pronotum at the base of the spiracular lobe (fig. 17 C), the second (56) a broad, fan-shaped muscle taking its origin on the ventral surface of the supraneural bridge of the endosternum (figs. 11 C, 12 C); both muscles are inserted close together on the coxal rim shortly behind the pleural articulation (fig. 13 D, 55, 56). The mesal remotor (57) is a slender muscle with its origin on the pleural apophysis (fig. 11 C) and its insertion on the posterior mesal angle of the coxal base (fig. 13 C, D).

The sixth muscle of the fore coxa (fig. 13 C, D, G, 58) comes from the mesothorax, where it arises on the anterior part of the median sternal ridge that supports the superstructure of the pterothoracic endosternum (fig. 22 C); it extends horizontally forward and laterally (fig. 12 C, 58) to its insertion on a small point of the coxal base mesad of the pleural articulation (fig. 13 D). The pull of this muscle can have little specific motor action on the coxa, but the two muscles diverging from the mesosternal ridge to the fore coxae are evidently retractors not only of the coxae but of the entire propectus, being thus adjuncts of the intersegmental ventral thoracic muscles (fig. 12 C, 52). The intersegmental coxal muscle is classed as an "extensor" of the coxa by Morison (1927), but the corresponding muscle in *Vespula*



is termed by Duncan (1939) the "mesosternal retractor of the propectus."

The coxae of the mesothorax are elongate and semicylindrical in form; each is attached by the entire length of one side to the under surface of the thorax behind the mesosternum, and the trochanter arises from its mesal end (figs. 15, 22 A, B). The mesocoxa is definitely hinged to the body between a lateral pleural articulation and a mesal sternal articulation (fig. 16 F); its axis of movement is obliquely transverse, with the mesal end somewhat in advance of the lateral end, and its movement is rotary on the axis.

The musculature of each middle coxa comprises two promotor muscles inserted at opposite ends of the coxa anterior to the axis of rotation, and two remotors with the same distribution behind the axis. The lateral promotor (fig. 22 C,  $\delta_0$ ) is a long muscle arising dorsally on the small pleural apophysis (*PLA*) of the mesothorax, and inserted on the anterior coxal rim a short distance from the pleural articulation (*d*). The small mesal promotor ( $\delta_1$ ) arises ventrally on the median plate of the pterothoracic endosternum, and is inserted on the anterior coxal margin near the sternal articulation (*e*). The lateral remotor of the mesocoxa ( $\delta_2$ ) is the muscle of the subalar epipleurite (*Sa*); it arises by a broad base on the posterior margin of the coxa just behind the pleural articulation, and is inserted by a long tendon on the subalare. This muscle probably has little effect as a motor of the coxa, but it would appear to be primarily a pleurocoxal muscle. The mesal remotor of the coxa ( $\delta_3$ ) is the largest of the coxal muscles; it arises on the median plate of the endosternum and is strongly attached mesally on the posterior coxal margin.

The metathoracic coxae (fig. 15) are hinged obliquely transverse between pleural and sternal articulations (fig. 16 F), as are the mesocoxae, but their bases are more nearly horizontal than are those of the latter, and the coxae themselves project posteriorly (fig. 24 A), with the trochanters arising from their distal ends.

The musculature of the metacoxae is the same as that of the mesocoxae, there being inserted on the base of each hind coxa four muscles (fig. 24 B), two of which, attached before the coxal axis (*d-e*), are, the one a lateral promotor ( $103$ ), the other a mesal promotor ( $104$ ), while a third inserted mesally behind the axis is a mesal remotor ( $106$ ). The fourth muscle ( $105$ ), as in the mesothorax, is the coxosubalar muscle of the wing; it is attached on the coxa so close to the pleural articulation (*d*) and so nearby on the line of the coxal axis that it can have little effect as a motor of the coxa.

The mesal promotor and the mesal remotor take their origins on the metathoracic basal components of the pterothoracic endosternum (fig. 24 A, 104, 106); the lateral promotor (103) arises on the ridge between the metapleuron and the propodeum.

*The coxo-trochanteral joint.*—The union between the coxa and the trochanter in each leg of the bee is a dicondylic hinge with an approximately horizontal anteroposterior axis. The movements of the trochanter on the coxa, therefore, are up and down, and are best expressed as *levation* and *depression*. In the bee the trochanter of each leg is provided with two levator muscles, one anterior, the other posterior, arising within the coxa, and with two or three depressors having a common point of insertion, but arising both in the coxa and within the thorax. The two levators are inserted directly on the trochanter or close to it; the fibers of the depressor muscles have no direct connection with the trochanter, but are inserted on a large depressor apodeme arising from a small plate in the ventral articular membrane at the base of the trochanter. The trochanteral muscles are the motors of the entire part of the leg (*telopodite*) beyond the coxa, the movements of which are in a plane at right angles to the coxal plane of movement.

In the fore leg the relatively small anterior and posterior levators of the trochanter (fig. 13 E, H, 59, 60) arising in the coxa are inserted on the trochanteral base just beyond the coxo-trochanteral articulations (E, *f*, *g*). The depressors include a long thoracic muscle (E, H, 61) arising on the prothoracic pleural apophysis (figs. 11 C, 12 C, 61), which is inserted on the end of the depressor apodeme of the trochanter (fig. 13 E, H), and a large group of fibers (62), arising on the mesal wall of the coxa, inserted on the sides of the apodeme and on the apodemal plate. Since the articular surfaces of the trochanter (E, *f*, *g*) are much closer to the insertions of the levator muscles than to the base of the depressor apodeme, the effectiveness of the large depressor muscles is greatly increased by their advantageous leverage.

In the mesothoracic legs the two levator muscles of each trochanter arise on the lower (lateral) wall of the coxa (fig. 22 D, 84, 85), and are inserted anteriorly and posteriorly on the base of the trochanter. The thoracic muscle of the depressor group (D, G, 86) takes its origin on the side of the endosternum (C); the coxal fibers are distinctly divided into two muscles (D, G, 87, 88), one anterior, the other posterior, separated by the pedal nerve (G, *Nv*) entering between them into the trochanter.

The trochanter of each hind leg has two large levator muscles (fig. 24 C, D, 107, 108), a long thoracic depressor (C, E, 109) arising on the metathoracic arm of the endosternum (A, 109), and a single, broad coxal depressor (C, E, 110). The levators (107, 108) are inserted in the dorsal articular membrane (D), the depressors (109, 110) on a long ventral apodeme (*Ap*).

*The trochantero-femoral joint.*—The hinge between the trochanter and the femur differs from all the other leg joints in that its axis traverses the vertical plane of the leg, and is, moreover, strongly oblique, the dorsal end being distal to the ventral end (figs. 13 H, 24 C). The movements of the femur on the trochanter, therefore, are those of *production* and *reduction*, but, owing to the obliquity of the hinge, the femur acquires also an upward slant as it turns backward. A single *reductor* muscle activates the femur.

The obliquity of the trochantero-femoral joint in the vertical plane of the leg gives the trochanter a firm pressure or hold on the femur in responding to the depressor and levator action of the trochanteral muscles, the trochanter and the femur being thus moved as a unit on the coxo-trochanteral articulation.

The character of the trochantero-femoral joint differs but little in the three legs of the bee. In each leg there is anteriorly a narrow hinge line between the two adjoining segments (figs. 13 H, 24 C), with an articular point (*h*) at the upper end; only in the hind leg is there a definite ventral articulation (fig. 24 C, F, *i*). Posteriorly the trochanter and femur are separated by a wide, thick, strongly elastic conjunctiva (fig. 13 B, *cnj*). The femoral reductor muscle (fig. 13 H, 63; fig. 22 D, G, 89; fig. 24 C, *III*) arises anteriorly by a broad base in the trochanter and its convergent fibers are inserted on a shelflike apodemal plate projecting from the posterior rim of the basal foramen of the femur (figs. 13 F, 24 F, *Ap*). The contraction of the muscle, therefore, turns the femur posteriorly on the anterior hinge with the trochanter; the muscle is opposed by the resistance of the elastic posterior conjunctiva, which restores the femur to its original position on relaxation of the reductor muscle.

*The femoro-tibial joint.*—The "knee" joint of each leg has strictly a hinge motion on a horizontal axis between anterior and posterior articulations. The movements of the tibia, therefore, are those of *extension* and *flexion* on the end of the femur; they are produced by dorsal and ventral muscles lying in the femur. The head of the tibia is somewhat bent toward the femur, and the hard wall of the femur is deeply emarginate below the joint, allowing the tibia to be flexed close against the femur.

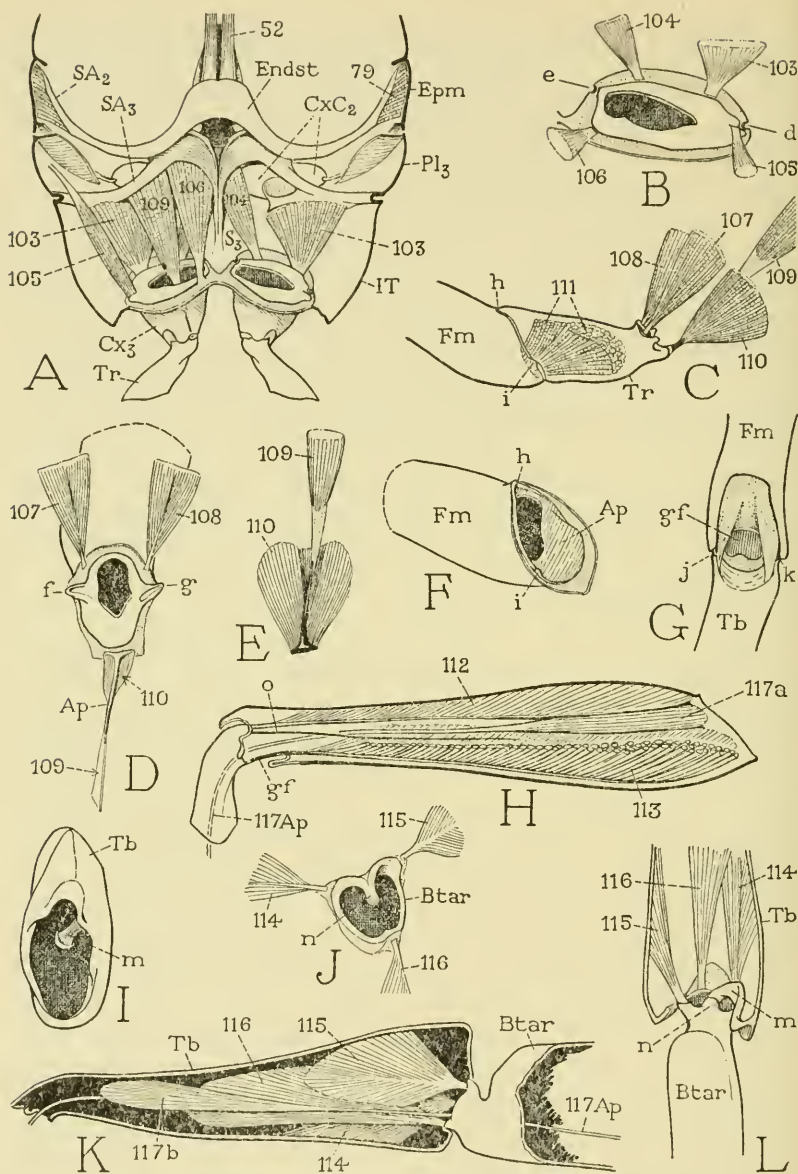


FIG. 24.—The metathoracic leg, muscles and joints (drone).

A, endosternum and ventral wall of posterior part of pterothorax, showing muscles of meta-thoracic coxae, dorsal view. B, base of right hind coxa and muscle insertions, dorsal view. C, right trochanter and base of femur, with trochanteral and femoral muscles, anterior (outer) view. D, proximal view of right trochanter and muscle insertions. E, depressor muscles of trochanter. F, base of right femur, anterior view. G, femoro-tibial joint of right hind leg, ventral view. H, right hind femur with muscles, anterior view. I, distal end of right tibia. J, proximal end of right basitarsus. K, right hind tibia and muscles, posterior view. L, tibio-tarsal joint of right hind leg, dorsal view.

d-e, pleurosternal axis of coxa; f, g, anterior and posterior coxal articular processes of trochanter; h, i, dorsal and ventral trochantero-femoral articulations; j, k, anterior and posterior femoro-tibial articulations; m, tibial articular process of tibio-tarsal joint; n, tarsal articular process of tibio-tarsal joint; o, ligament of femoral chordotonal organ.



The femoro-tibial joint differs but little in the three legs of the bee. Its mechanism is well exemplified in the middle leg, which, seen from below (fig. 22 J), shows the two articular points ( $j, k$ ) of the joint and the deep membranous ventral emargination of the wall of the femur. The articulations consist of two strong basal lobes of the tibia (L), which fit against corresponding processes concealed within the end of the femur (K,  $j, k$ ). The conjunctival membrane below the joint (H, J) contains a small, partly invaginated *genuflexor plate* ( $gf$ ), to the apex of which is attached the tendon of the broad, pin-nate flexor muscle of the tibia ( $\rho I$ ) lying ventrally in the femur. The fibers of the extensor muscle arise along the dorsal wall of the femur (H,  $\rho o$ ), and are inserted on an axial tendon attached to the recurved dorsal head of the tibia (H, L). In the hind leg the joint structures are essentially the same as in the middle leg, though somewhat different in shape (fig. 24 G), and the tibial muscles are larger (H,  $II2, II3$ ).

The femur of each leg contains in addition to the tibial muscles a branch of the flexor muscle of the pretarsal claws (fig. 24 H,  $II7a$ ), which is inserted on the end of a long tendon ( $II7Ap$ ) extending through the tibia and tarsus. Finally, there is to be found in each femur a slender, tendinous thread ( $o$ ) attached on the head of the tibia just anterior to the extensor tendon (fig. 22 L), which extends proximally in the femur, and probably belongs to a chordotonal organ such as occurs in the femur of various other insects.

*The tibio-tarsal joint.*—The joint between the tibia and the tarsus in each leg of the bee is quite different from that between any of the other leg segments; it is monocondylic, and the tarsus is movable on the tibia by three muscles. The single point of articulation is median and dorsal, but is concealed within the distal end of the tibia; two of the muscles are inserted respectively anterior and posterior to the articulation, the third muscle is ventral.

The essential features of the tibio-tarsal joint are the same in all three legs, but structural details and the mechanism are somewhat different in the hind legs. In the first and the second leg the proximal end of the long basitarsus presents dorsally three knobs (fig. 22 E). The middle knob ( $n$ ) is the articular condyle; it is received on the concave surface of a large, hook-shaped articular process ( $m$ ) that descends from the dorsal wall inside the end of the tibia (I,  $m$ ). The lateral knobs give attachment to the anterior and posterior tibial muscles (E,  $\rho2, \rho3$ ), which arise on the corresponding walls of the tibia. In the fore leg and the middle leg the attachments of these muscles on the tibia are so nearly on a level with the articular condyle



that the anterior muscle (92) acts as a *productor* of the tarsus, and the posterior muscle (93) as a *reductor* when tension is exerted on the muscles in a dead specimen. Morison (1927) calls these two muscles anterior and posterior "extensors" of the tarsus, but if they have an extensor effect on the tarsus, the action is weak. The third tarsal muscle arises on the lower wall of the tibia (fig. 22 F, I, 94) and is attached by an axial tendon in the ventral conjunctival membrane of the joint. This muscle unquestionably is a depressor of the tarsus. The opposite movement of the tarsus, if not produced by the lateral muscles, must result from the elasticity of the articular conjunctiva. In the fore leg the tibio-tarsal joint mechanism operates the antenna cleaner.

The tibio-tarsal joint of the hind leg, as above mentioned, differs in some ways from that of the other legs. The articular condyle of the basitarsus is a long, curved arm descending from the dorsal rim of the proximal tarsal foramen (fig. 24 J, *n*); the corresponding articular process of the tibia (I, *m*) is a strong sclerotization of the anterior wall of the tarsal socket in the end of the tibia (L, *m*), which curves inward over the tendon of the anterior muscle (114), dips downward, and turns distally to articulate ventrally with the lower end of the tarsal condyle (*n*). The articulation of the two segments is thus almost at the center of the tarsal foramen. As a consequence, the attachment of the posterior tarsal muscle (J, K, L, 115) is so far above the level of the articulation that this muscle, representing the tarsal reductor in the other legs, becomes in the hind leg a strong *levator* of the tarsus. The anterior muscle (114), being inserted nearly opposite the articular point, is evidently a *productor*; the ventral muscle (116) is the tarsal depressor.

The structure of the tibio-tarsal joint of the hind leg is the same in both the drone and the worker, and hence has no direct relation to the pollen press of the latter. The mechanism of the joint in the hind leg, however, especially the combined levator-productor action of the two lateral muscles, is unquestionably conducive to the effective action of the press.

*The tarsal joints.*—The narrowed base of each of the small tarsal subsegments, or tarsomeres, beyond the large basitarsus fits into a receptive cavity in the end of the preceding tarsomere (fig. 23 G), and each of these joints is monocondylic, as is the tibio-tarsal joint itself. The dorsal lip of the minute basal foramen of each small tarsomere is drawn out into a long articular process, which fits into a socket formed by an inward extension of the lip of the distal foramen of the tarsomere preceding. There are no intratarsal muscles giving

individual movement to the tarsomeres, but the entire tarsus is traversed by the flexor-muscle tendon (*117Ap*) of the pretarsal claws, and a pull on this tendon causes a deflexion of the slender part of the tarsus beyond the basitarsus.

*The pretarsus.*—The pretarsus of the honey bee has a complex and highly specialized structure (fig. 25 A, B). The median part of the segment is differentiated into a conical, stalklike basal part (E) from which the claws arise laterally, and an oval distal lobe, which is the arolium (*Ar*). In the ordinary position of the foot (E) the arolium stands upward between the claws on the end of the basal support. Dorsally the arolium presents a deep concavity (A) between its up-turned lateral parts, and in its outer wall is a dark, elastic, U-shaped band, the *arcus* (B, E, *arc*), which embraces the base of the arolium ventrally with its arms extending distally in the lateral walls. The conical base of the pretarsus contains dorsally an elongate median sclerite (A, E, *mn*) armed with five or six long, thick, curved spines. By its widened base the sclerite is articulated to the end of the tarsus between the bases of the claws, and its narrowed distal end is attached like a handle to the base of the scoop-shaped arolium (H), for which reason the sclerite may be termed the *aroliar manubrium*. In the ventral wall of the pretarsal base is a broad, weakly sclerotized plate, the *planta* (B, E, *pln*), thickly beset with strong spines diverging distally.

The claws are hollow, strongly sclerotized lateral outgrowths of the membranous lateral walls of the pretarsal base. Each claw has two points of unequal length, and in size and shape the claws differ considerably as between the drone (fig. 25 A, B) and the worker (C, D). Dorsally the claws are articulated individually to two small knobs on the end of the tarsus (A, *o*, *p*), corresponding with the articular condyles at other dicondylic joints of the leg, but the claws themselves are devoid of muscles.

The motor apparatus both of the claws and of the arolium consists of the depressor muscle of the pretarsus, and of accessory sclerites in the ventral articular membrane at the base of the segment. The principal one of the basal sclerites is a large median plate, known as the *unguitractor plate* (fig. 25 B, *Utr*), which is comparable with the genuflexor plate below the knee joint. In the membrane at the proximal end of the unguitractor plate is attached the tendon of the pretarsal muscle (*95Ap*), and at the distal angles are two small *auxiliary sclerites* (*aux*) intermediate between the unguitractor plate and the bases of the claws. The pretarsal tendon extends forward through the tarsus (fig. 23 G) into the tibia (fig. 24 K), where it

divides into two branches, one branch giving insertion to a group of fibers arising posteriorly in the tibia (*117b*), the other, going on into the femur, to a second group (*H*, *117a*) arising posteriorly in

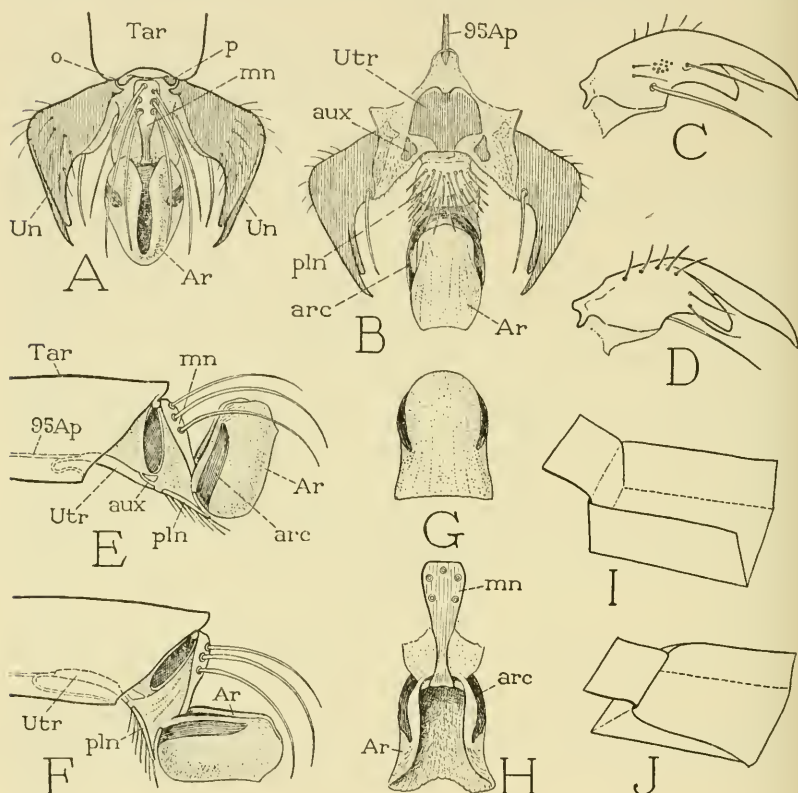


FIG. 25.—The pretarsus.

A, pretarsus of middle leg of drone, dorsal surface, flattened, inner sides of claws uppermost, arolium turned upward. B, same, ventral surface, arolium depressed and spread out. C, posterior claw of middle leg of worker, outer surface. D, anterior claw of hind leg of worker, inner surface. E, pretarsus and end of tarsus, claws removed, arolium turned upward, semidiagrammatic. F, same, arolium depressed. G, ventral surface of fully depressed and flattened arolium. H, arolium and manubrium, dorsal view. I, paper model of arolium and manubrium in nonfunctional condition. J, same, illustrating flattening of arolium by downward pressure on manubrium.

95Ap, tendonlike apodeme of muscle of pretarsus (retractor of the claws); Ar, arolium; arc, arcus; aux, auxilia; mn, manubrium; o, p, anterior and posterior tarso-pretarsal articulations; pln, planta; Tar, end of fifth tarsomere; Un, claw (unguis); Utr, unguitractor plate.

the base of the femur. The tension of the pretarsal muscle on the unguitractor plate is distributed to the claws through the auxiliary sclerites, and thus flexes the claws, for which reason the muscle is

known as the *flexor of the claws*. The direct effect of the muscle pull, however, is exerted on the base of the pretarsus, and, unless the claws interfere, it flexes the pretarsus on the end of the tarsus (fig. 25 F) and brings the arolium into a horizontal position.

The arolium is an organ that enables the bee to cling to smooth surfaces on which the claws cannot hold. When the arolium is in use as an adhesive organ the claws are turned proximally with their points directed outward, and the arolium is horizontally extended, its lateral walls spread out flat, its under surface (fig. 25 G) pressed against the support. The extension and flattening of the arolium has been explained by Arnhart (1923; see Snodgrass, 1925) as caused by a secretion liquid forced into the foot from a gland in the end of the tarsus; but a study of the mechanism of the pretarsus shows that the action of the arolium including its changes in shape can be produced entirely by mechanical means.

With a live bee it may be observed that when the flexing claws encounter on a smooth surface nothing to restrain them or to give them a hold, they turn helplessly upward beneath the end of the tarsus with their points sprawling outward. The tension of the contracting pretarsal muscle is then exerted on the base of the pretarsus, which turns abruptly downward bringing the arolium into a horizontal position, after which the arolium extends, spreads out flat, and clings to the support. If the foot of a dead bee is in the position shown at F of figure 25, an upward pressure on the retracted planta (*pln*) extends the pretarsus until the planta comes into the same horizontal plane as the arolium (*Ar*), and now, with continued pressure, the arolium itself automatically unfolds and spreads out with its flattened under surface downward. This action of the arolium can be induced by manipulation of a detached pretarsus, in which there can be no possibility of liquid pressure from within the tarsus. The same kind of action, moreover, can be illustrated with a piece of paper cut and folded into the form of a scoop (I); a vertical compression of the base of the scoop spreads the sides widely apart (J), giving thus a close imitation of the partly expanded arolium (H).

The similar response of the arolium to pressure against the planta is evidently caused in the living bee by the downward pressure of the tarsus, which flattens the pretarsus and compresses the arolium against the support beneath it. The manubrial sclerite of the pretarsus (fig. 25 E, H, *mn*), however, representing the handle of the paper scoop (I, J), plays an important part in the expansion of the arolium. With the extension of the foot, the manubrium turns backward on the end of the tarsus and hence pushes on the upper edge of the aroliar



base, thus augmenting the effect of the pressure on the planta; finally, when fully extended, the manubrium clamps down on the arolium and holds it securely in the spread condition. There can be little doubt, therefore, that the entire action of the arolium is a mechanical result of the pull of the pretarsal muscle in conjunction with pressure of the foot against the support when the claws fail to take a hold on the latter. It has been said that the arolium adheres to smooth surfaces by means of a sticky exudation from the spines of the planta, but observation fails to reveal the presence of any such adhesive. The upper surface of the arolium is covered with minute hairs, but its under surface is almost entirely bare.

## VI. THE ABDOMINAL PETIOLE

The outstanding feature in the external organization of the clistogastrous Hymenoptera is the secondary consolidation of the fourth body segment with the thorax, and the division of the body by a deep constriction between the fourth and fifth segments, accompanied by a narrowing and usually an elongation of the anterior end of the fifth segment, or even of the entire segment, to form a *petiole*. Two important mechanical advantages result from these alterations, which take place during the pupal stage of development. First is the greatly increased length that the dorsal wing muscles of the thorax are able to acquire by a posterior extension of the mesothoracic postphragma into the fourth segment (fig. 16 C); second is the high degree of potential mobility conferred on the shortened abdomen. The first advantage is self-evident, the second needs elucidation.

In the more generalized insects the abdomen is broadly attached to the thorax by its first segment, and the muscles that move the abdomen as a whole are dorsal and ventral intersegmental muscles between the metathorax and the abdomen. In winged insects, however, the dorsal intersegmental muscles of the metathorax become functionally a part of the flight mechanism (fig. 26 A,  $d_3$ ) by a transfer of the ridge or phragma of their abdominal attachment to the thorax. As a consequence, the dorsal metathoracic muscles of winged insects have no motor effect on the abdomen. Ventral muscles between the thorax and the abdomen are seldom strongly developed, and they may be absent; when present they comprise generally one pair or two pairs of slender muscles arising anteriorly on the metasternal apophyses and attached posteriorly sometimes on the first abdominal sternum (A), but more commonly for greater effectiveness on the second (C) or even the third, fourth, or fifth sternal plate.



Such insects have little mobility of the abdomen on the thorax, even though the two parts of the body may be separated by a constriction.

A comparison of the structural relation between the thorax and the abdomen in clistogastrous Hymenoptera (fig. 26 B) with that in

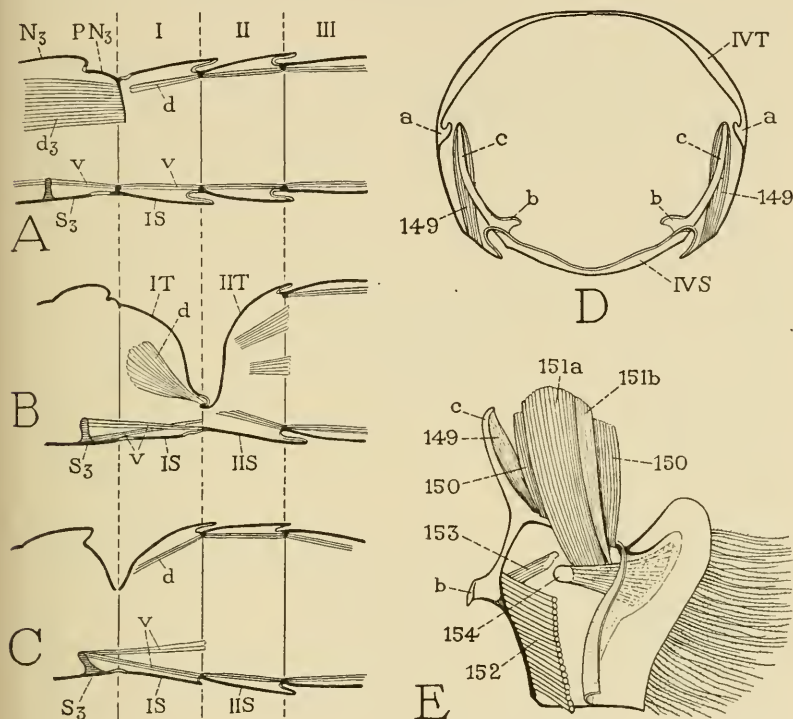


FIG. 26.—Relation between the propodeum and the abdominal petiole; lateral muscles of an abdominal segment.

A, diagram of thoraco-abdominal relation in a generalized winged insect: the dorsal intersegmental muscles of metathorax ( $d_3$ ) are wing motors and do not move the abdomen. B, specialized condition in clistogastrous Hymenoptera: dorsal and ventral muscles ( $d$ ,  $v$ ) of first abdominal segment (propodeum) become effective motors of rest of abdomen. C, usual structure in higher winged insects: abdomen but little movable on thorax. D, anterior end-view of abdominal segment IV of drone, showing mechanism of dorsoventral expansion by contraction of reversed anterior lateral muscles. E, right half of abdominal sternum IV of drone, with sternal and lateral muscles.

$a$ , anterior tergal apodeme;  $b$ , anterior sternal apodeme;  $c$ , lateral sternal apodeme;  $d$ , dorsal intersegmental muscles;  $v$ , ventral intersegmental muscles.

either a generalized winged insect (A) or a more specialized form (C) will show clearly the advantage derived by the Clistogastra from having the first abdominal segment solidly joined to the thorax, and a constricted point of movement established between the first and

second segments of the abdomen. The modification allows the muscles of the transposed first abdominal segment (*B, d, v*) to become effective motors of the free part of the abdomen. The aculeate Hymenoptera thereby acquire a much greater abdominal mobility for the use of the ovipositor or sting or for mating activities than is possessed by any other insects.

The mechanism of the clistogastrous petiole is well illustrated in the honey bee, though the petiole itself in the bee is relatively short. Particular attention to the petiole as an important part of the organization of the bee was first given by Betts (1923), who fully describes its structure and its principal muscles. The propodeum and the first segment of the functional abdomen are joined by a membranous conjunctiva (fig. 27 A, C), which permits freedom of movement of the abdomen on the propodeum, but the two parts are hinged dorsally by a pair of articular points (*C, f, f*). Between the articular points on the dorsal surface of the petiole is a small elevation of the conjunctival membrane (*e*) connecting anteriorly with a notch in the end of the propodeum (*t*). Within this swelling of the conjunctiva is a dorsal pocket of the anterior end of the petiole (*D, F, G*) having a strongly sclerotic floor supporting a median ridge (*D, F, r*). Ventrally (*A, E*) the conjunctiva is a wide membrane between the weak sternal plate of the propodeum (*IS*) and the sternal plate of the petiole (*IIS*). The muscles that move the abdomen as a whole are attached dorsally, laterally, and ventrally on the narrowed end of the petiole (*G*); they represent dorsal intersegmental muscles between the primarily first and second abdominal segments (fig. 26 A, B, C, *d*), and ventral intersegmental muscles of the metathorax (*B, C, v*) that pass over the first abdominal sternum to attach on the second.

The petiole muscles of the honey bee include two pairs of dorsal muscles and two pairs of ventral muscles, but on account of the positions of their attachment on the petiole, one pair of the dorsal muscles are levators of the abdomen, one pair of ventrals are depressors, and the other two pairs evidently produce sidewise movements. The levator muscles arise by broad, spreading bases on the lateral walls of the propodeum (figs. 27 B, C, 28 A, 120), and are inserted by strong tendons that converge to their attachments on the posterior end of the ridge on the floor of the petiole pocket (fig. 27 D, F, G). These muscles thus acquire a short leverage on the propodeal fulcrum (*f*). The depressors of the abdomen are a pair of long ventral muscles arising on the metathoracic components of the pterothoracic endosternum (fig. 27 E, 118), and inserted medially on the

anterior margin of the sternal plate of the petiole (E, G). The lateral muscles of the petiole include a pair of two-branched dorsal muscles arising anteriorly on the sides of the propodeum (figs. 27 B, 28 A, 121) and inserted on the lateral angles of the tergum of the petiole

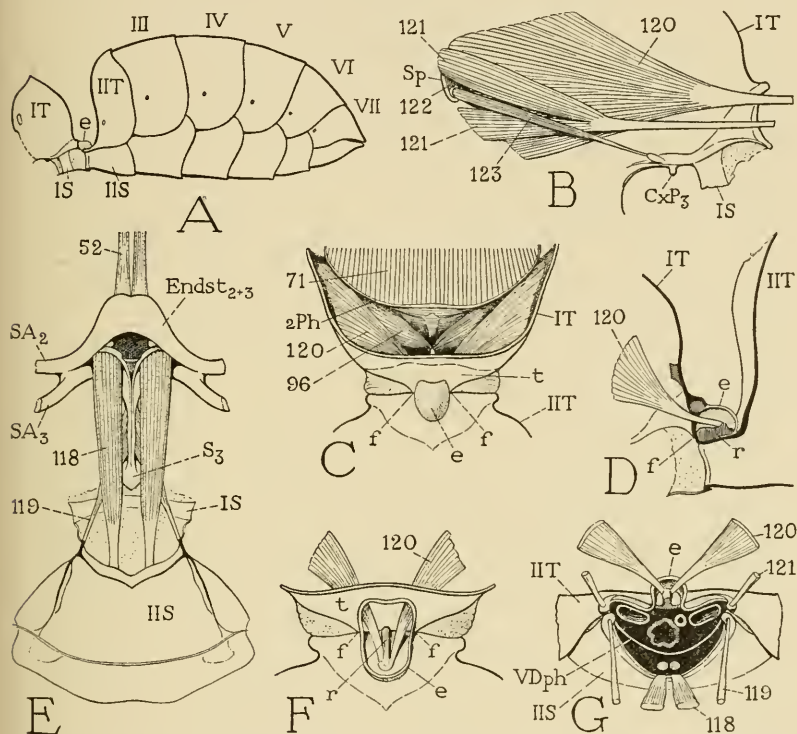


FIG. 27.—The propodeum and petiole. (Figures, except E, from Snodgrass, 1933.)

A, abdomen of worker, including propodeum. B, muscles in right side of propodeum, mesal view. C, propodeum and petiole, dorsal wall of propodeum removed, exposing muscles. D, levator mechanism of abdomen exposed by removal of left wall of propodeum and petiole. E, ventral muscles of petiole, dorsal view. F, petiole and end of propodeum, dorsal view, upper wall of petiolar pocket (*e*) removed to show insertion of levator muscles (120). G, anterior end of petiole, showing muscle attachments on tergal and sternal plates.

*e*, membranous roof of dorsal pocket of petiole; *f, f*, fulcrum of movement of abdomen on propodeum; *r*, median ridge on floor of petiolar pocket; *t*, posterior area of propodeum adjoining petiole.

(fig. 27 G), and a pair of ventral muscles arising on the metathoracic sternum (E, 119), which are inserted laterally on the end of the petiole sternum (E, G). The cavity of the neck of the petiole is divided transversely by the ventral diaphragm (G, *VDph*), which

begins in the metathorax. The larger dorsal channel gives passage to the tracheal trunks, the oesophagus, and the aorta; the ventral channel contains the nerve cords.

## VII. THE ABDOMEN

Structural changes in an animal that bring about conditions in conflict with standardized nomenclature create embarrassing situations for the descriptive anatomist. The transfer of the fourth body segment to the thorax in the Clistogastra, for example, leaves us without a suitable term for the third region of the body in this group of Hymenoptera, since the body region called the "abdomen" in all other insects includes the transposed segment of the Clistogastra. The clistogastrous abdomen has been termed the *postabdomen*, and the *gaster*, but neither name is satisfactory; the first is used also for the last four or five segments in certain insects in which the posterior genital region of the abdomen is structurally differentiated from the anterior visceral region, and the word "gaster" ordinarily refers to the stomach. The most practical solution of the difficulty for hymenopterists is to use the term *abdomen* in a functional rather than a morphological sense for the third body region of the insect. The abdomen in the Clistogastra, therefore, is not entirely homologous with that of the Chalastogastra, and to keep in view the identity of the segments in the two groups the primary abdominal segments may be designated *I* to *X* regardless of their associations. Segment *I* in the Clistogastra is the thoracic propodeum, segment *II* is the segment of the abdominal petiole, segment *X* is the anus-bearing lobe or tube known as the *proctiger*. In many Hymenoptera the true anus lies within a terminal invagination of the proctiger, which possibly represents segment *XI*.

*General structure of the abdomen.*—The segments of the pregenital region of the abdomen in the honey bee have well-developed tergal and sternal plates, but there are no lateral, or "pleural," sclerites, and the spiracles lie in the sides of the terga (fig. 27 A). The tergal plates, except the first, are provided each with a large *anterior tergal apodeme* on each side (figs. 26 D, 28 A, 29 A, *a*); the sternal plates have each a pair of *anterior sternal apodemes* (figs. 26 D, 28 A, B, 29 A, *b*), and on each side a long *lateral sternal apodeme* (*c*). The sternal plates of segments *III* to *VI* widely underlap each the sternum of the following segment, forming pockets which in the worker conceal the areas of the wax glands on sterna *IV* to *VII*.



In the male bee the dorsum of the exposed part of the abdomen ends with the declivous tergal plate of segment *VIII* (fig. 29 A), but the sternum of this segment (*VIIIS*) is concealed within that of segment *VII*, and the visible part of the venter terminates with sternum *IX*. The tergum of segment *IX*, however, is represented only by a pair of small dorsal sclerites lying at the sides of the proctiger (figs. 29 A, 30 A, *IXT*), each of which supports internally a large apodeme (fig. 29 A, *ap*) giving attachment to the dorsal muscles of its segment (B). The sternum of segment *IX* (figs. 29 A, 30 A, B, *IXS*) is a relatively large crescentic plate exposed beyond sternum *VII*, and bears on its posterior margin the two pairs of phallic plates (*lp*, *pv*). The proctiger is a membranous lobe (fig. 30 A, *Ptgr*) with a small subanal plate (*b*) in its ventral wall between the two sclerites of the ninth tergum.

In the queen and the worker bee the exposed part of the abdomen ends with the tergum and the sternum of segment *VII* (fig. 27 A). The margins of the apical plates are ordinarily closed upon each other, concealing a large invagination cavity that contains segments *VIII* and *IX*, the proctiger, and the sting. Segment *VIII* is a complete annulus at the base of the cavity, but its walls are membranous except for two lateral remnants of the tergum, which contain the spiracles and are associated with the base of the sting. The tergites of segment *VIII*, therefore, are known as the *spiracular plates* of the sting (fig. 28 C, *VIIIT*). In the posterior wall of the ventral part of the eighth segment is a depression containing the female genital openings (D). Segment *IX* supports the sting, but it is hardly to be recognized as a segment; its only sclerotized parts are two lateral tergal plates that form virtually a part of the stinging apparatus (fig. 31 A, *Qd*), and are hence called, because of their position and shape, the *quadrate plates* of the sting. The venter of the ninth segment (*IX.V*) is entirely membranous and, when the sting is retracted, is mostly concealed between the oblong plates (*Ob*) of the basal apparatus of the sting.

*The abdominal musculature.*—The musculature of the abdomen follows a definite plan, the pattern of which is repeated alike in each of the segments, except for omissions in the first and the last three segments, and the addition of a few special muscles in connection with the genital organs and the sting. The typical segmental musculature is complete in segments *III* to *VI* in both sexes, but the individual muscles of the male (fig. 29 B) are much larger than those of the female (fig. 28 A). The somatic abdominal muscles, exclusive



of the muscles of the dorsal and ventral diaphragms, may be classed as intertergal *dorsal muscles*, tergosternal *lateral muscles*, intersternal *ventral muscles*, and *spiracular muscles*. The dorsals and ventrals again include internal and external groups of fibers, and the internal dorsal and ventral muscles comprise median and lateral muscles.

For a study of the abdominal musculature segment *V* of the worker may be taken as a representative segment (fig. 28 A, *V*), the larger muscles of the drone (fig. 29 B) being less isolated. On each side of the tergum of segment *V* two bands of muscle fibers diverge posteriorly to attach on the antecosta (*Ac*) of tergum *VI*. These muscles are the internal dorsals, one median (155), the other lateral (156). The single short external dorsal (157) is a reversed muscle, since it arises posteriorly on tergum *V* and extends forward to its insertion on the anterior apodeme (*a*) of tergum *VI*. The spiracular muscles include a small occlusor (not seen in the figure) attached at both ends on the spiracle itself, as shown in segment *VII* (C, 180), and a long, slender dilator (A, 159) arising on the lateral apodeme of the sternum (*c*). Of the three tergosternal lateral muscles, the first (160) is a reversed muscle arising ventrally on the lower part of the tergum and inserted dorsally on the long lateral apodeme of the sternum (fig. 26 D, 149). The other two lateral muscles cross each other obliquely in the female (fig. 28 A) from the tergum to the sternum, the one which is external (161) being attached on the sternal margin, the other (162) on the posterolateral upper surface of the sternum. In the male (figs. 26 E, 29 B) the second and third lateral muscles are parallel. The external muscle is a broad band of fibers (fig. 26 E, 150) attached on the sternal margin; the internal lateral muscle includes two distinct groups of fibers (151a, 151b), the second distinguished by its pale, whitish color, both attached on the upper surface of the posterior part of the sternum. The sternal musculature duplicates the pattern of the tergal musculature, there being a pair of posteriorly divergent internal ventrals on each side (fig. 28 A, B, 163, 164), and a single reversed external ventral (A, 165) between the overlapping parts of the consecutive sterna.

Functionally the internal dorsal and ventral muscles are *contractors* of the abdomen, inasmuch as they retract the individual tergal and sternal plates. The external dorsal and ventral muscles of the more posterior segments, on the other hand, are *extensors* of the abdomen, since their contraction protracts the segmental plates by reducing the overlap between them. Similarly, the reversed muscles of the lateral series are *dilators* of the abdomen (fig. 26 D, 149), because their contraction separates the tergum and the sternum of each segment,

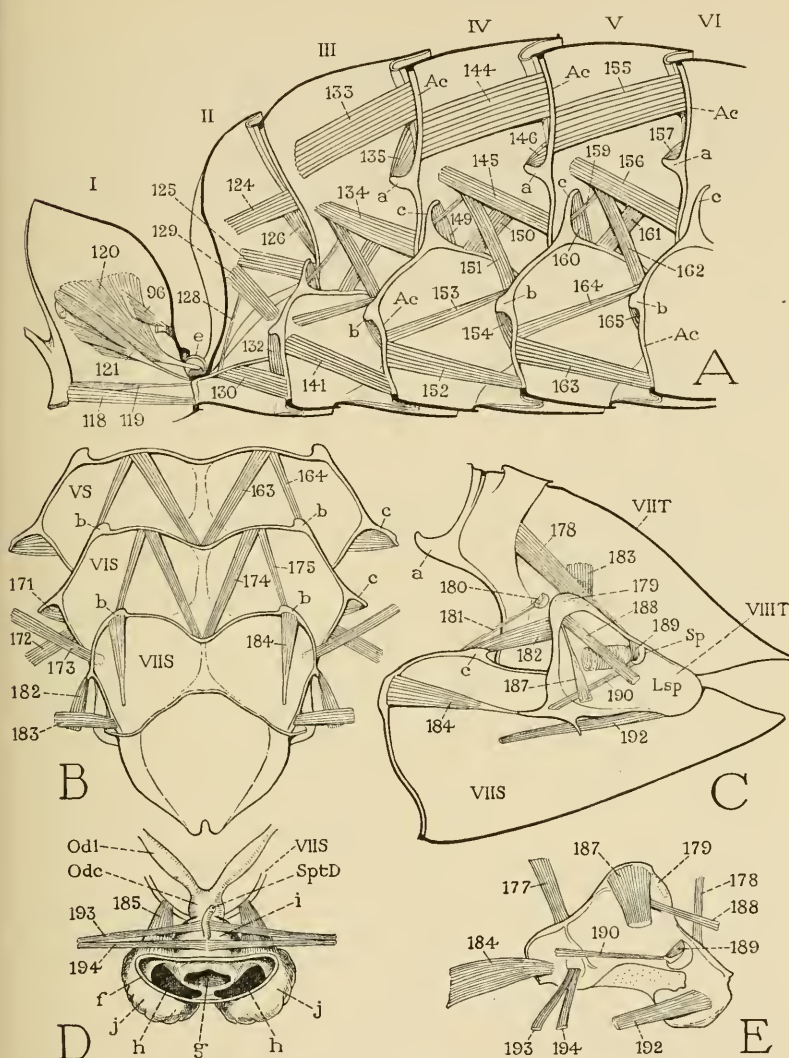


FIG. 28.—The abdominal musculature of the worker and queen. (From Snodgrass, 1933, with muscles renumbered.)

A, muscles in right half of anterior part of abdomen of worker, including propodeum, mesal view. B, ventral muscles of abdominal segments *V*, *VI*, and *VII* of worker, dorsal view. C, muscles of right half of segment *VII* and of spiracular plate of segment *VIII* of worker, mesal view. D, genital pouches and oviducts of queen, with attached muscles, posterodorsal view. E, right spiracular plate of segment *VIII* of queen, and its muscles, mesal view.

*a*, anterior tergal apodeme; *b*, anterior sternal apodeme; *c*, lateral sternal apodeme; *e*, dorsal pocket of petiole; *f*, edge of shallow external part of genital chamber; *g*, vaginal aperture (opening of median genital pouch); *h*, *h*, apertures of lateral genital pouches; *i*, median pouch (vagina) of genital chamber; *j*, *j*, lateral pouches of genital chamber.

and thus expands the abdomen dorsoventrally. The other lateral muscles pull the tergal and sternal plates together and are therefore *compressors* of the abdomen. The entire musculature of the pre-genital segments is operative in respiration, since the abdominal breathing movements of the bee are both dorsoventral and longitudinal. The same muscles, however, produce various other movements of the abdomen, and it would appear that the dorsal and ventral muscles, or the lateral muscles of opposite sides may act either in unison or as antagonists. Finally, it should be noted that the external dorsal and ventral muscles in the more anterior segments of the abdomen (fig. 28 A, 126, 132, 135) run obliquely or transversely between the adjoining segmental plates, and thus evidently produce a partial rotary or *torsion* movement of the anterior segments on each other.

The musculature of the petiole segment (fig. 28 A, II) is simplified by the absence of the first and second lateral muscles and, in the worker, of the lateral internal ventral, though this muscle is present in the drone (fig. 29 B, 131).

In segments VII, VIII, and IX the musculature is progressively reduced and altered as these segments become involved in modifications adaptive to the reproductive functions. In the drone (fig. 29 B) segment VII retains the typical dorsal musculature, but the second pair of lateral muscles is absent, and the sternum has on each side only a small lateral internal muscle (B, D, 186) attached posteriorly on the long anterior apodemal arm (*b*) of sternum VIII. In segment VIII of the drone there is on each side a single, short dorsal muscle (B, 187) attached posteriorly on the apodeme of the ninth tergal sclerite (*IXT*), one lateral muscle (191), and a short lateral internal ventral (B, D, 195) between the eighth sternum and the small parameral plate (*lp*) of the genital apparatus. Segment IX has only one pair of short dorsal muscles (B, 202) from the apodemes of the ninth tergal plates to the base of the proctiger at the sides of the subanal plate, but there are two small phallic muscles on each side (D, 203, 204) arising ventrally on the parameral plate (*lp*) and attached dorsally on the arm of the penis valve (*pv*), while finally a long slender muscle (205) goes from the arm of the penis valve to the mucus gland, to which it is attached just laterad of the termination of the vas deferens.

In the female the musculature as well as the structure of the posterior abdominal segments is very different from that of the male. The tergal musculature of segment VII in the worker includes on each side an internal dorsal (fig. 28 C, 178) attached on the upper

margin of the spiracular plate of segment *VIII* (*VIIIT*), and a reversed lateral lying external to the spiracular plate and attached on the upper angle of the latter (179). In the queen there are two internal dorsal muscles of segment *VII* (E, 177, 178) attached on the spiracular plate. The lateral musculature consists of two tergo-sternal muscles on each side (C, 182, 183), and a very small reversed muscle, not shown in the figures. The sternum of segment *VII* in the worker (C) has none of the usual ventral muscles, but in the queen a pair of median internal ventrals is present (D, 185) attached posteriorly on the copulatory pouch. In both the worker and the queen, however, there is a large, intersegmental sternotergal muscle (C, 184) arising anteriorly on sternum *VII* and attached posteriorly on the lower anterior angle of the spiracular plate (C, E).

The muscles of segment *VIII* in the female all take their origins on the spiracular plates, which are lateral remnants of the eighth tergum. On each side two dorsal muscles (fig. 28 C, E, 187, 188) arise in the upper angle of the spiracular plate and go to the corresponding quadrate plate of the sting, which represents the tergum of segment *IX*. Each spiracle has the usual occlusor (189) and dilator (190) muscles, but the dilator arises on the spiracular plate, there being no sternal plate in the eighth segment. From the lower edge of each spiracular plate a long posterior muscle (192) goes forward to the triangular plate of the sting (fig. 31 B, D, 192), and in the queen two slender anterior ventral muscles (fig. 28 E, 193, 194) go mesally to the dorsal wall of the vagina (D).

The muscles of segment *IX* in the female pertain to the sting, except two small muscles from the quadrate plate to the ventral wall of the proctiger (fig. 31 B, 200, 201). The other muscles will be described in connection with the sting.

*The male genital organ.*—The phallic organ of the Apidae differs from that of all other Hymenoptera in a reduction of the outer parts and a great development of the endophallic sack. In *Apis mellifera* the ectophallic parts consist of two pairs of small plates lying behind the last abdominal sternum (fig. 30 A, B, C, D, *lp*, *pv*), the small outer pair of which (*lp*) may be identified with the *parameral plates*, and the larger inner pair (*pv*) with the *aedeagal plates*, or *penis valves*, of other families (see Snodgrass, 1941). Between the penis valves and thick membranous folds uniting them dorsally and ventrally is a widely distensible opening, the *phallotreme* (*Phtr*), which leads into the cavity of a huge endophallic invagination (F, *Enph*) that extends forward as far as the segment of the petiole.



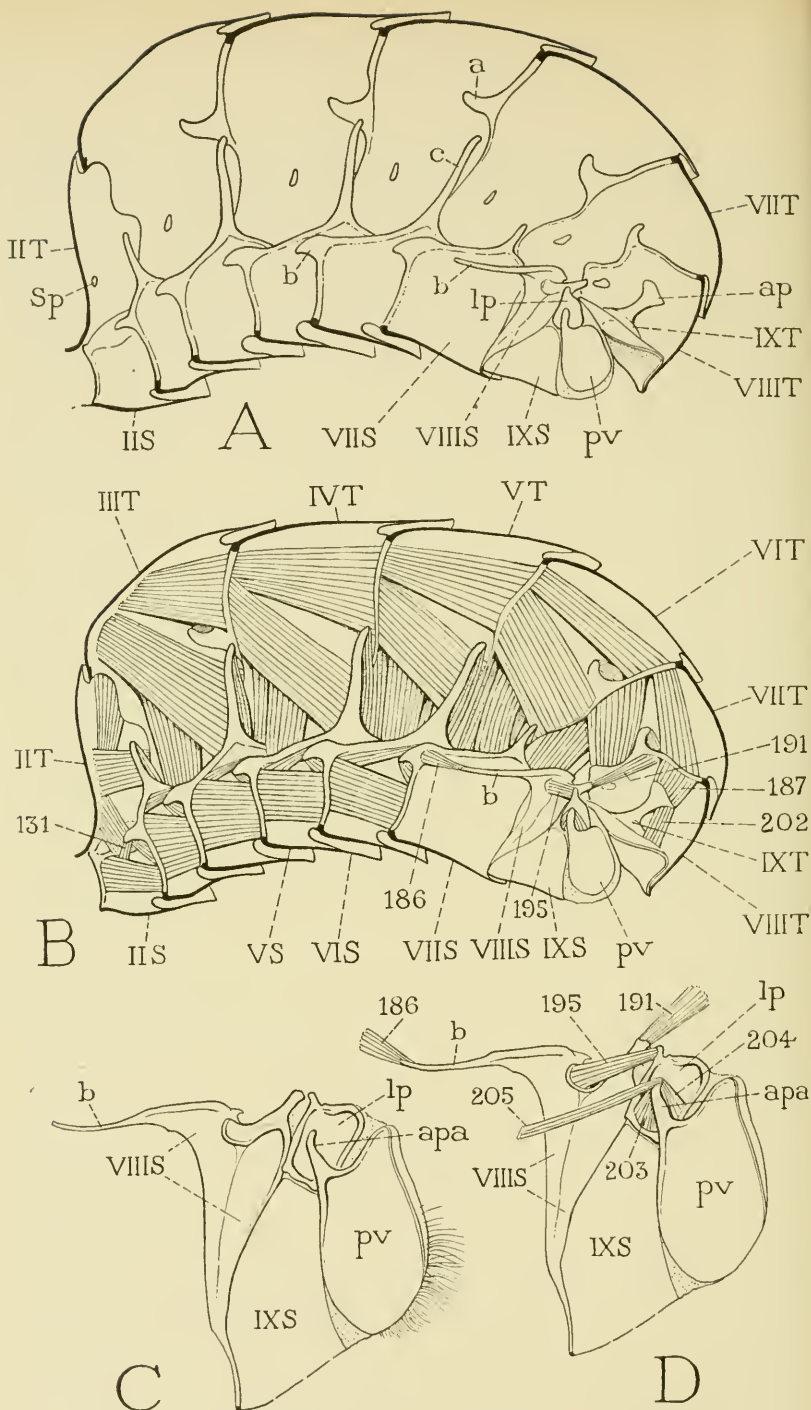


FIG. 29.—The abdominal musculature of the drone, not including the pro-podeum. (From Snodgrass, 1941, with muscles renumbered.)

A, right half of abdominal wall, mesal view. B, muscles of right half of abdomen, mesal view. C, right halves of sternal plates of abdominal segments *VIII* and *IX*, and right phallic plates, mesal view. D, same, with muscles.

*a*, anterior tergal apodeme; *b*, anterior sternal apodeme; *c*, lateral sternal apodeme.



The endophallus is the intromittent organ of the bee; during mating it is everted, in part or entirely, and inserted into the genital tract of the queen. Structurally the endophallus is differentiated into three major sections: first, opening directly from the phallotreme, is a large sack, or *bursa* (fig. 30, F, *Brs*); the second, middle part is a narrowed neck, or *cervix* (*Cer*), connecting the bursa with the third, innermost part, which is a large, thick-walled *bulb* (*Blb*). The ejaculatory duct (*Dej*) opens into the anterior end of the bulb.

The endophallic bursa (fig. 30 F, *Brs*) has tough membranous walls, which are more or less collapsed and folded in the retracted condition. From the sides of the bursa project a pair of large, tapering, thin-walled, crumpled *cornua*, or *pneumapophyses* (*bc*). In the ventral wall are two somewhat elevated dark areas, the first (*c*) quadrate in form, the second (*d*) shield-shaped. Internally these areas are seen to be flat pockets of the bursal wall covered with a dense growth of small, dark spines or thick curved hairs. Elsewhere the inner walls of the bursa are closely dotted with minute spicules, but the linings of the cornua are bare, though wrinkled and finely alveolate in appearance.

The cervix of the endophallus is ordinarily compressed into an irregular shape (fig. 30 F, *Cer*), but when stretched out straight it is seen to be a wide tube with tough membranous walls. Along the length of its lower wall runs a rounded fold (*e*) that forms internally a ventral gutterlike channel. Externally the fold is crossed by a series of V-shaped elevations conspicuous by their dark color, which is due to an internal covering of small spines. Similarly, an internal spine-covered patch at the posterior end of the dorsal wall appears externally as a triangular or cordate dark area (*f*). Near its anterior end the cervix bears dorsally a large diverticulum (*flb*), known as the *pinnate*, or *fimbriate, lobe* because its margins are deeply cut into flat, overlapping lobules.

The large endophallic bulb (fig. 30 F, *Blb*) has a complex structure, which is not fully understood since it has never been thoroughly studied by histological methods. In the distal half of its dorsal wall are two parallel, elongate, strongly sclerotic plates (E, F, *g*), which are usually shown in illustrations as external structures, but they are covered by a thin outer tunic that forms a fold in the groove between them and is continued over the rest of the bulb. The plates, therefore, would appear to be sclerotizations of the inner wall of a flat dorsal pouch of the bulb lumen; when the covering tunic is removed the smooth outer surfaces of the plates are exposed (E) and the tapering posterior ends are seen to project freely into the posterior part of

the cavity of the bulb. The plates are not separable from a large spongy body beneath them that forms the dorsal wall of the bulb cavity and thins out on the sides, where it is continued into a chitinous intima covering the rest of the lumen. From the inner wall of the spongy body two small, posterior triangular plates (*E, h*) project laterad of the dorsal plates as free flaps into the cavity of the bulb.

In most drones taken in late summer the endophallic bulb is found to be filled with a dense mass of spermatozoa and fine granular matter, which, in specimens preserved in alcohol, forms a compact body molded into the shape of the interior of the bulb (fig. 30 H). This body is termed by Zander (1911) a *Samenpatrone* ("seminal cartridge," *cartouche* of Leuenberger, 1929). It is not, however, a true spermatophore, or sperm-containing capsule, since it has no retaining wall; its outer surface in preserved specimens is dense and regular, but is minutely pilose because of the great number of sperm tails projecting from it.

The discharge of the spermatozoa is accomplished by eversion of the endophallus. The endophallic walls being entirely nonmuscular, eversion of the organ is brought about naturally by a strong muscular compression of the abdomen, and this function of the abdomen in the male probably accounts for the great size of the abdominal muscles of the drone (fig. 29 B) as compared with those of the queen or worker (fig. 28 A). Artificially a partial evagination of the endophallus is easily produced in a fresh specimen by pressure on the abdomen, and is often seen in killed specimens (fig. 30 G). Bishop (1920), however, describes methods by which a complete eversion can be induced, and Leuenberger (1929, fig. 17) gives a photograph of the fully everted organ.

In the first stage of the endophallic eversion, or the condition usually produced by artificial compression of the abdomen, the bursa is turned entirely inside out (fig. 30 G, *Brs*) with the everted cornua (*bc*) projecting upward and outward from its sides. The stretched cervix of the organ now traverses the lumen of the bursa and opens between the bases of the cornua. It is generally supposed (though apparently never observed) that in the copulatory act the cornua, or pneumapophyses, enter the lateral pouches of the female genital chamber (fig. 28 D, *j*); probably the cervical aperture on the distended bursa is held close to the opening of the median vaginal pouch (*g*), and the endophallic bulb then everted through the cervix into the vagina. Zander (1911) contended that the bulb is not everted, since in newly mated queens he found it in the uneverted condition grasped between the base of the ovipositor and the seventh abdominal sternum. On

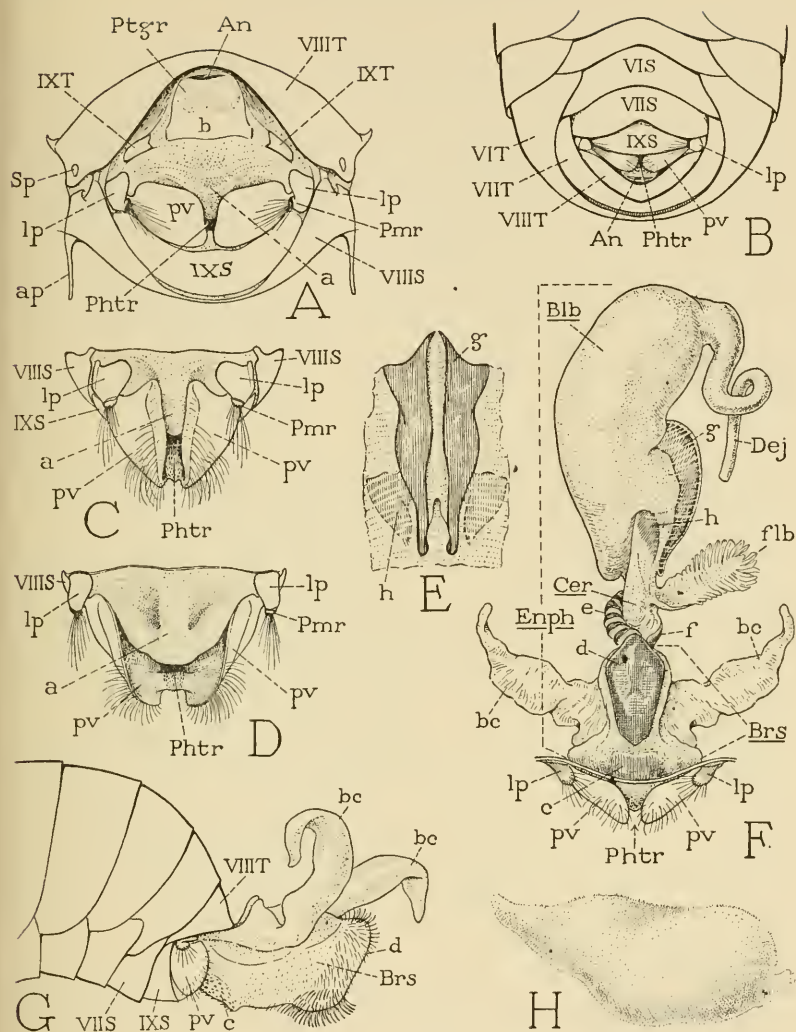


FIG. 30.—The male genitalia. (Figures A to F from Snodgrass, 1941.)

A, segments VIII, IX, and X of male abdomen, end view, showing phallotreme and genital plates between sternum IX and proctiger. B, end of male abdomen, ventral view. C, ectophallus, dorsal view. D, same, phallotreme distended by separation of penis valves (*pv*). E, dorsal and inner plates of endophallic bulb. F, ectophallus and invaginated endophallus, dorsal view. G, end of abdomen with endophallus partly everted. H, mass of spermatozoa and agglutinating material in bulb of endophallus.

*a*, membranous dorsal lip of phallotreme; *An*, anus; *ap*, anterior apodeme of sternum VIII; *b*, subanal plate of proctiger; *bc*, bursal cornua; *Blb*, bulb of endophallus; *Brs*, bursa of endophallus; *c*, spiny area of inner bursal wall; *Cer*, neck of endophallus; *d*, setigerous area of inner bursal wall; *Dej*, ductus ejaculatorius; *e*, corrugations of endophallic neck; *Enph*, endophallus; *f*, setigerous area of inner wall of endophallic neck; *flb*, fimbriate lobe; *g*, dorsal plate of endophallic bulb; *h*, inner plate of bulb; *lp*, lamina parameralis; *Phtr*, phallotreme; *Pmr*, paramere; *Ptgr*, proctiger; *pv*, penis valve.

the other hand, Shafer (1917) describes four cases in which he observed the bulb everted and contained within the vagina. Both writers agree that the bulb has an inverted position in the queen, and Shafer notes that the reversed points of the dorsal plates of the bulb are pressed upward against the vaginal wall, thereby preventing an extraction of the bulb. Only the bulb is said to be found adhering to a mated queen, the other parts of the male organ, the cervix and the bursa, probably being torn away when the queen detaches herself from the drone. Both Shafer and Bishop believed that the spermatozoa are discharged into the vagina directly from the exposed end of the ejaculatory duct, but according to Zander the sperm are already stored in the bulb at the time of mating. The observations recorded above on the presence of a spermiatic mass in the bulb of unmated drones suggests that the condition described by Zander is true probably in most cases. Differences in the age of drones examined may account for the observed presence or absence of spermatozoa in the bulb.

The mating of the honey bee is a subject that still needs investigation. We know nothing definitely concerning the function of the various structural parts of the complex endophallic organ of the drone, and, notwithstanding evidence that the bulb is everted into the vagina, it is difficult to imagine how such a thick-walled structure can be turned inside out.

*The sting.*—The sting of the bee has been so many times described that only a summarized account of its structure and mechanism need be given here; the writer has elsewhere (1933) given a full discussion of both phases of the subject. Though the hymenopterous sting is a modified ovipositor, its parts have long been known to students of the honey bee under special names, and these names will be used in the following description.

The act of stinging involves movements of the entire abdomen that accomplish the initial thrust of the shaft of the sting into the skin of the victim. The farther penetration of the shaft into the wound and the injection of the poison are produced by movements of the sting itself. The stinging organ (fig. 31 A) comprises two distinct parts: one is a large basal part by which the sting is attached within the sting chamber at the end of the abdomen, and which constitutes the motor apparatus; the other is the long, tapering shaft, which is the effective part of the organ, and is alone protracted from the abdomen during the act of stinging. The two parts of the sting are connected anteriorly by a pair of curved, flexible arms, and in the position of rest the shaft lies beneath the basal part and is mostly concealed within the latter.



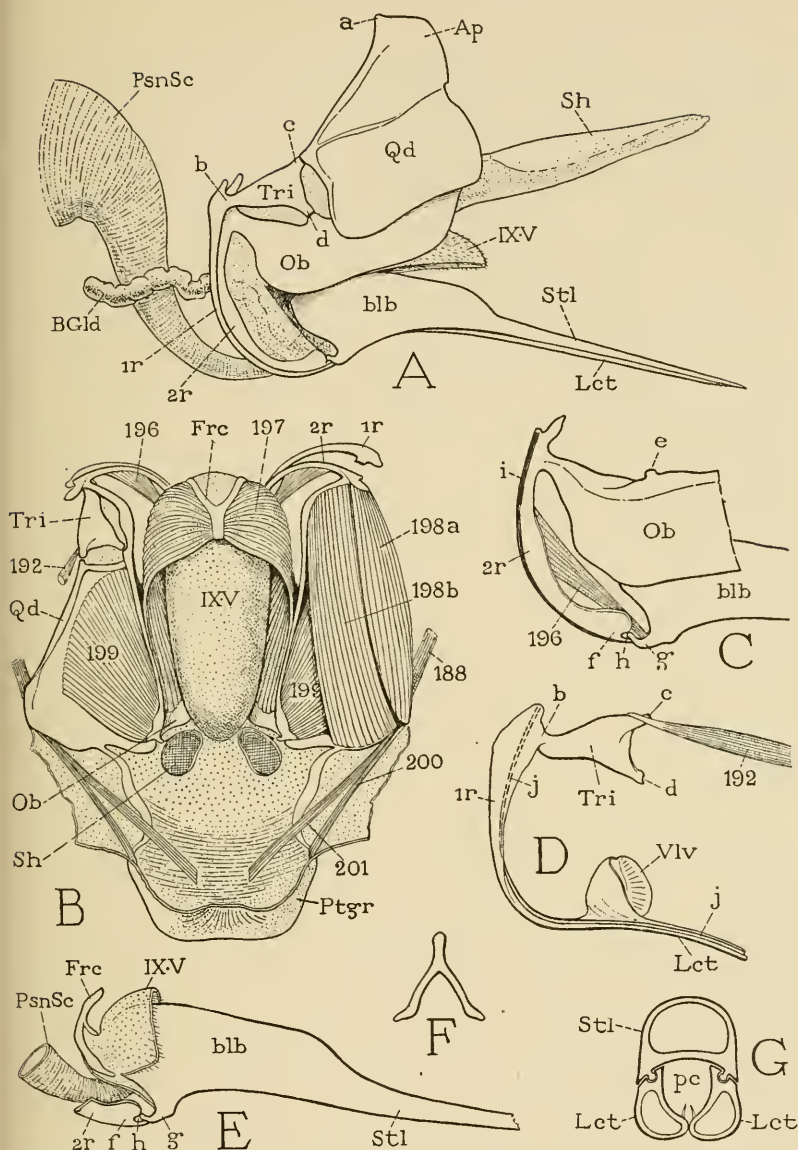


FIG. 31.—Structure of the sting. (From Snodgrass, 1933, with muscles re-numbered.)

A, sting of worker, lateral view. B, sting and its muscles, with ventral wall of proctiger, dorsal view. C, bases of oblong plate and bulb of stylet connected by second ramus (*2r*). D, triangular plate and base of lancet connected by first ramus (*1r*). E, proximal bulbous part of stylet, showing basal articulation on second ramus, attachment of furcula, and entrance of duct of poison sack into base of bulb. F, furcula. G, cross section of distal part of shaft of sting.

*a*, angle of attachment of quadrate plate to spiracular plate of eighth segment; *Ap*, apodeme of quadrate plate; *b*, apex of triangular plate; *BGld*, "alkaline" gland of sting; *blb*, bulb of stylet; *c*, *d*, basal angles of triangular plate; *e*, fulcrum of triangular plate on oblong plate; *f*, articular lobe of second ramus; *Frc*, furcula; *g*, articular lobe of bulb; *h*, hinge between second ramus and bulb; *i*, ridge of second ramus; *j*, groove of first ramus; *Lct*, lancet; *Ob*, oblong plate; *pc*, poison canal; *PsnSc*, poison sack; *Ptgr*, proctiger; *Qd*, quadrate plate; *1r*, first ramus (basal arm of lancet); *2r*, second ramus (basal arm of stylet); *Sh*, sheath lobe; *Stl*, stylet; *Tri*, triangular plate.



The basal apparatus of the sting presents on each side three plates (fig. 31 A). Uppermost is the large *quadrate plate* (*Qd*), which, as already explained, is a lateral remnant of the ninth abdominal tergum. Below the quadrate plate, and partly overlapped by its lower margin, is a horizontally elongate *oblong plate* (*Ob*). Above the anterior end of the oblong plate and before the quadrate plate is a small *triangular plate* (*Tri*), articulated by the dorsal angle of its base (*c*) with the quadrate plate, and by the lower angle (*d*) with the upper edge of the oblong plate. The triangular plate and the oblong plate represent, respectively, the first and the second valvifer of the ovipositor of other insects. Projecting from the distal end of each oblong plate is a long, soft appendage (*Sh*); the pair of appendages clasp the shaft of the retracted sting and thus form a *sheath* for the latter. Between the lower edges of the oblong plates is a deeply concave membranous fold, which is the unsclerotized ventral wall of segment *IX*; it projects posteriorly as a free lobe (*IX.V*) when the shaft is depressed.

The shaft of the sting consists of three closely appressed parts mutually tapering to a point (fig. 31 A). The unpaired upper component is the *stylet* (*Stl*), the paired lower elements the *lancets* (*Lct*). The lancets are the so-called first valvulae of an ovipositor, the stylet represents the united second valvulae. Proximally the stylet is expanded in a bulblike enlargement (*blb*), which contains a cavity open below and continued as a ventral groove to the end of the stylet. The curved arms that unite the shaft with the supporting base of the sting are composed each of two parts. The first (*1r*) is a proximal *ramus of the lancet*, connecting the lancet with the apical angle (*b*) of the triangular plate (*Tri*); the second (*2r*) is a corresponding *ramus* of the stylet connecting the base of the stylet bulb with the anterior end of the oblong plate (*Ob*). The slender lancets are held close to the under surface of the stylet by grooves that fit over tracklike ridges of the latter (*G*), and the same interlocking apparatus is continued upon the basal rami, the first ramus being grooved to its upper end (*D, j*), the second having a ridge on its convex margin (*C, i*). The lancets are thus able to slide freely back and forth on the under side of the stylet. Between the stylet and the lancets is the poison canal of the sting (*G, pc*), which expands proximally into the cavity of the bulb, and here receives the poison liquid from the great poison sack (*A, PsnSc*), or reservoir of the poison glands, which opens into the base of the bulb. Each lancet bears on its proximal part a valvelike lobe (*D, Vlw*), the two lobes projecting side by side into the cavity of the bulb, where they serve

to propel the poison through the poison canal when the sting is in action. Finally we must note a small forked rod, the *furcula* (E, *Frc*, F), that projects into the body cavity at the base of the bulb above the neck of the poison sack. The furcula is an apodermal structure giving attachment to important muscles of the sting (B, *Frc*).

When the sting is not in use it is concealed within the abdomen, where its base is supported in the membranous wall of the sting chamber, and the upper angles of the quadrate plates are loosely articulated on the spiracular plates of the eighth segment (fig. 32 A). The shaft is turned upward on the rami so that the bulb is encased in the membranous fold between the oblong plates, and the distal part is clasped by the sheath lobes. When the sting goes into action, the whole structure is swung downward and posteriorly on the dorsal angles of the quadrate plates (*a*) until the basal apparatus takes a ventral position with the sheath lobes directed upward (fig. 32 B); simultaneously the shaft is depressed and, by the backward swing of the sting base, is protracted from the tip of the abdomen. The lancets now begin a rapid, alternate back-and-forth movement on the stylet. The action of the sting thus involves three separate movements: first the backward swing of the entire organ, second the depression of the shaft, third the movement of the lancets. On retraction of the sting, the shaft is replaced in the sheath, and the base returns to the position of repose.

The backward swing of the entire organ in the sting chamber was attributed by the writer in a former paper (1933) to pressure supposedly engendered within the abdomen by contraction of the abdominal segments. More recently, however, Rietschel (1937) has shown that specifically it is the depression of the seventh abdominal sternum that projects the sting. Manipulation of a dead specimen, in fact, will demonstrate that when the seventh sternum is turned downward, its broad anterior part, turning upward and backward, is pressed deeply into the abdomen against the base of the sting and forces the latter to swing posteriorly. The shaft, of course, is not protracted by this action, since it must at the same time be turned at right angles to the supporting apparatus. The depression of the shaft is effected by a pair of large, flat muscles arising on the inner surfaces of the oblong plates (fig. 31 B, 197) that curve anteriorly and mesally over the base of the bulb and are inserted on the furcula (*Frc*). The tension of these muscles on the furcula pulls upward on the base of the bulb (fig. 32 C), and the shaft is turned downward on a pair of fulcral points (*h*) at the lower angles of the bulb that abut against small lobes on the lower ends of the second rami (*ar*). The fulcral

apparatus is shown in greater detail at C and E of figure 31, and the action of the depressor muscles (197) on the shaft is diagrammatically expressed at D and E of figure 32. Mesad of the fulcrum each ramus of the stylet is continuous with the bulb by a slender, flexible connection. The opposite movement of the shaft, by which it is again turned upward and ensheathed between the oblong plates and their distal appendages, is effected by a pair of slender muscles stretched from the second rami to the fulcral lobes of the bulb (figs. 31 B, C, 32 C, D, 196), the insertion points of the muscles being sufficiently beyond the fulcral points to afford a short leverage on the shaft.

The movements of the lancets accomplish the penetration of the tip of the shaft into the victim, and the injection of the poison into the wound. They are produced by two pairs of large muscles in the basal apparatus that affect primarily the quadrate plates, and secondarily the triangular plates and the attached lancets. The muscles of one pair consist each of two large bundles of fibers (figs. 31 B, 32 C, 198) attached posteriorly, one laterally the other mesally, on the upper apodemal part of the quadrate plate, and anteriorly on the anterior end of the oblong plate. The muscles of the other pair (199) are attached anteriorly by broad, spreading bases on the inner surfaces of the quadrate plates, and posteriorly on the posterior ends of the oblong plates. The alternate contraction of these two muscles on each side pulls the corresponding quadrate plate first forward and then backward, relative to the oblong plate; the movements of the quadrate plate are transmitted to the triangular plate (fig. 31 A, *Tri*) by the connection of the former with the upper basal angle of the latter (*c*); the triangular plate, in turn, rotates on its ventral articulation (*d*) with the oblong plate, and the final result is that the alternate up-and-down movement of the apical angle (*b*) of the triangular plate is transmitted to the attached ramus of the lancet (*lr*), which gives the lancet itself a back-and-forth movement on the stylet. The mechanism is illustrated diagrammatically at F and G of figure 32. At F muscle 199, the *retractor of the stylet*, is contracted, the quadrate plate consequently pulled backward, the apex of the triangular plate lifted, and the lancet (*Lct*) retracted by the pull on its basal ramus. At G muscle 198, the *protractor of the lancet*, is in contraction, the quadrate plate is pulled forward, the triangular plate depressed, and the lancet protracted. In a living bee, as may be seen in a freshly extracted sting, the movements of the quadrate plates appear as a rapid vibration, and the two lancets have alternately opposite motions.





do so even when the sting is detached from the body of the bee. At the same time the contents of the poison sack are poured into the bulb of the sting and driven through the poison canal by the action of the valves on the bases of the lancets. The poison escapes through a ventral cleft near the tips of the lancets.

### VIII. ANNOTATED LIST OF MUSCLES

The terms *origin* and *insertion* are conventional in descriptive myology for denoting muscle attachments respectively at the fixed and the movable ends of the muscle. Literally there is no "insertion" of insect muscles, the muscle fibers being attached directly on the integument by means of cuticular *tonofibrillae*. Insect *tendons*, moreover, are merely slender apodemal ingrowths of the integument. The incongruous expression "inserted on" has thus become current in entomological writing, referring in some cases to the muscle attachment proper by tonofibrillae, in others to the attachment of the apodemal tendon on the integument.

In the following list of the bee's muscles reference is made principally to the work of Morison (1927) on the muscles of the honey bee, and to that of Duncan (1939) on the wasp. Citations of the more fragmentary work of earlier writers are given by Morison, in part by the writer (1933, 1941), and need not be repeated. In general there will be no difficulty in identifying the muscles listed here with those described by Morison, notwithstanding differences in functional names; a few discrepancies are noted.

1. *Adductor of the labrum*.—A slender muscle arising on the frontal region between bases of antennae, inserted by a long tendon laterally on posterior margin of base of labrum. (*Levator labri* Morison.)

2, 3, 4, 5. *Extrinsic muscles of the antenna* (fig. 2 A, C).—Four muscles arising on anterior arm of tentorium, inserted on base of antenna.

6. *Levator of the antennal flagellum* (fig. 2 H).—A slender muscle arising on dorsal wall of scape, inserted dorsally on base of pedicel.

7. *Depressor of the antennal flagellum* (fig. 2 H).—Origin on ventral wall of scape, insertion ventrally on base of pedicel.

8. *Abductor of the mandible* (fig. 3 I).—A flat muscle arising by spreading fibers on genal and postgenal walls of cranium behind lower part of compound eye, inserted by strong apodeme in membrane between mandibular base and pleurostomal margin of cranium (fig. 3 E, 8Ap).



9. *Adductor of the mandible* (fig. 3 H).—A larger muscle than the last, fibers arising in several groups behind upper part of compound eye, on postgena below level of foramen magnum, and one small group (9a) on top of head, inserted by strong apodeme in articular membrane mesad of mandibular base (fig. 1 C, 9Ap).

10. *Promotor of the maxilla; cardinal protractor of the proboscis* (fig. 4 A).—Origin posteriorly on inner face of postgenal inflection forming lateral wall of proboscis fossa, inserted on short arm of cardo beyond articular process.

11, 12, 13. *Adductors of the maxilla; stipital protractors of the proboscis* (fig. 4 A).—Three muscles arising on extreme anterior end of anterior tentorial arm, 11 inserted on proximal end of stipes, 12 and 13 on mesal margin of stipes. These muscles are primarily adductors of the maxilla, but because of the angulation between cardo and stipes they become protractors, and in the bee protract the entire proboscis.

14. *Muscle of the maxillary palpus* (fig. 4 B, F).—A large muscle arising in stipes (F), inserted on base of palpus. Morison describes this muscle as an extensor of the galea inserted on the base of the latter near the palpus. In *Vespula*, according to Duncan, there are two muscles with a common insertion on the palpus.

15. *Flexor of the galea* (fig. 4 F).—A large pinnate muscle arising posteriorly in stipes, inserted by long tendon laterally on base of galea. The galea of the bee, as in insects generally, has no extensor muscle.

16. *Flexor of the lacinia; tensor of the lacinial lobe* (fig. 4 F, G).—Origin in base of stipes, insertion on lever in base of lacinia; tension of this muscle on the lever raises the lacinial lobe (lcl) and holds it taut. (*Spanner des Segelhalters* Wolff; *flexor of the lacinia* Duncan; not given by Morison.)

17. *Anterior adductor of the labium; retractor of the proboscis* (fig. 7 A, D).—A long muscle arising on dorsal wall of cranium, tapering downward to strong tendon inserted on distal end of ligular bar of prementum (h). It retracts the entire proboscis, also the ligula into the prementum, and recurves the glossal tongue. (*Retractor linguae longus* Wolff; *retractor ligulae superior* Morison; *flexor of the paraglossa* Duncan.)

18. *Posterior adductor of the labium; protractor of the labium* (fig. 7 D).—Origin on extreme anterior end of anterior tentorial arm, inserted with muscle of opposite side by common tendon attached on base of prementum. Serves to adduct the labium, and probably also protracts it by flattening the angle between prementum

and postmentum. (*Protractor labii* Morison; *posterior labial adductor* Duncan.)

19. *Premental retractor of the ligula* (fig. 7 A).—Arises laterally in base of prementum, tapers to tendinous insertion on ligular arm (*h*) of prementum just laterad of 17. This muscle is probably the paraglossal muscle of the labium; functionally it is accessory to 17 in retraction of the ligula. (*Retractor linguae brevis* Wolff; *anterior flexor of the ligula* Duncan; wrongly described by Morison as *flexor palpi maxillaris*.)

20. *Flexor of the glossa, retractor of the tongue* (fig. 7 A, B).—Origin posteriorly in base of prementum, insertion by long tendon close to side of base of glossal rod. The muscles of this pair serve to shorten the tongue or to roll it from side to side. (Smaller branch of *retractor linguae biceps* Wolff; *retractor ligulae inferior* Morison; *posterior flexor of the ligula* Duncan.)

21. *Flexor of the labial palpus* (fig. 8 A).—A flat pinniform muscle arising on side of prementum, inserted by long tendon on rod in posterior wall of palpiger. It depresses the palpus and folds the latter back behind the stipes. (*Extensor palpi maxillaris* Morison; *depressor of the labial palpus* Duncan. Morison mistakenly assigns two muscles to the labial palpus in the bee. Duncan finds but one in *Vespa*.)

22. *Muscle of the second segment of the labial palpus* (fig. 8 A).—Origin in base of first palpus segment, insertion on base of second segment; flexes the second segment mesally, opposed by elasticity of the joint.

23. *Dilator of the salivary syringe* (fig. 7 A, C).—A flat muscle arising on anterior lateral margin of prementum, inserted medially on anterior wall of salivary syringe. (*Protractor linguae* Wolff; *dilator ampullae superior* Morison; *dilator of the salivarium* Duncan.)

24. *Compressor of the salivary syringe* (fig. 7 A, C).—Largest muscle in prementum, arising proximally, inserted distally on lateral margins of salivary syringe. Probably compresses the syringe by lateral tension. (Principal branch of *retractor linguae biceps* Wolff; *dilator ampullae salivae posterior* Morison; *posterior muscle of salivarium* Duncan.)

25. *Retractor, or levator, of the epipharynx* (fig. 10 C).—A group of fibers arising on distal part of clypeus, diverging to insertions within the epipharynx. (*Levator veli palatini* Wolff.)

26, 27, 28, 29, 30. *Dilators of the suctorium* (fig. 10 C).—Five large, paired bundles of short fibers arising on clypeus and inserted on anterior wall of cibarial region of sucking pump.

31. *Compressors of the suctorium* (fig. 10 C).—Five thick bundles of fibers on anterior wall of cibarial region of sucking pump, the first transverse over the mouth, the others oblique between the dilators, attached laterally on oral plate (*opl*).

32. *Protractor of the oral plate* (fig. 10 B, C).—Origin ventrally on a process of frontal aspect of base of anterior tentorial arm, insertion dorsally on upper part of pharyngeal arm (*y*) of oral plate above frontal ganglion connective. (*Lateral pharyngeal muscle* Duncan.)

33. *Retractor of the oral plate* (fig. 10 B, C).—A smaller muscle than the last arising medially on frons below median ocellus, inserted ventrally opposite 32 on arm of oral plate. (No corresponding muscle given by Duncan in the wasp.)

34, 35. *Precerebral dilators of the pharynx* (fig. 10 C).—Two small muscles arising on frons, inserted on pharyngeal region of sucking pump just above frontal ganglion. (*Frontal dilators of the anterior pharynx* Duncan.)

36. *Postcerebral muscle of the pharynx* (fig. 10 C).—Long slender muscle arising on vertex, inserted laterally on upper extremity of pharynx, probably mainly suspensory in function. (*Dorsal dilator of the posterior pharynx* Duncan.)

37. *Posterior contractor of the pharynx* (fig. 10 C).—A long, median, fusiform muscle lying against posterior wall of pharynx, arising by slender tendon on median process of tentorial bridge, inserted ventrally on inner edge of oral plate. (*Posterior dilator of the anterior pharynx* Duncan.)

38. *Parietal contractor of the pharynx* (fig. 10 C).—A broad sheet of fibers spreading over lateral and posterior walls of pharynx from two points of origin laterally on tentorial bridge, fibers going beneath circular muscles on lower half of pharynx to attachments on arms of oral plate. This muscle and the last are termed "dilators" of the pharynx in the wasp by Duncan, but their lengthwise distribution would suggest that they are contractors of the pharynx, though at the same time they may dilate the cibarium.

39. *Constrictors of the pharynx* (fig. 10 C).—The layer of circular fibers investing the entire pharyngeal region of the sucking pump, continued on the oesophagus.

40. *Superior phragmatic levator of the head* (fig. 12 A).—One of a pair of submedian, parallel muscles arising on prephragma of mesonotum, inserted laterally on dorsal margin of foramen magnum. (*Levator capitis horizontalis* Morison.)

41. *Inferior phragmatic levator of the head* (fig. 12 A).—One of a pair of long muscles arising laterally on prephragma of mesonotum, converging beneath 40 to insertion in dorsal angle of foramen magnum. (*Rotator capitis superior* Morison.)

42. *Pleural levator, or rotator, of the head* (fig. 12 B, D).—A large, three-branched muscle arising on episternum, inserted by common tendon attached in laterodorsal notch of foramen magnum; none of its fibers observed to arise on endosternum as stated by Morison. (*Rotator capitis inferior* Morison; *pleural elevator of the head* Duncan.)

43. *Endosternal levator, or rotator, of the head* (fig. 12 B, C).—A large muscle with wide base on dorsal surface of prothoracic endosternum, fibers convergent on long thick tendon attached in laterodorsal notch of foramen magnum above 42. (*Levator capitis obliquus* Morison; *furcal elevator of the head* Duncan.)

44. *Depressor of the head* (fig. 12 B).—A large muscle of two parts arising on dorsal surface of prothoracic endosternum anterior to 43, inserted by strong tendon on ventral margin of foramen magnum. (*Depressor capitis horizontalis* Morison; *first and second depressors of the head* Duncan.)

45. *Intersegmental dorsal muscle of the prothorax* (figs. 11 F, 12 A).—A thick muscle arising on middle of pronotum, attached posteriorly on prephragma of mesonotum; probably depresses the pronotum. (*Depressor prothoracis* Morison; *inner pronotal retractor of the mesonotum* Duncan.)

46. *Phragmatopleural muscle of the prothorax* (fig. 12 A).—Arises farthest laterad on prephragma of mesonotum, attached anteriorly on cervical apodeme of pleuron. (Lateral branch of *levator prothoracis internus* Morison; *anterior notal elevator of the propleuron and head* Duncan.)

47. A small prothoracic muscle attached close to 46 on cervical apodeme of pleuron (fig. 12 A, B) may be a branch of 48, though its fibers appear to run along the under side of the latter.

48. *Tergoepisternal muscle of the prothorax* (fig. 12 A).—A large, straplike muscle arising mesally on posterior inflection of pronotum (not on phragma), attached anteriorly on horizontal apodeme of episternum (A, B). (*Levator prothoracis externus* Morison.)

49, 50. *Protractors of the propectus* (fig. 12 B, C).—Two fan-shaped muscles arising anteriorly on side of pronotum, inserted on apex of pleural apophysis. (*Depressor episterni prothoracis anterior and posterior* Morison; *first and second posterior notal protractors of the propleuron* Duncan.)



51. *Adductor of the propleuron* (fig. 12 B).—A large muscle arising mesally on straplike apodeme of prothoracic endosternum (fig. 11 E, n), inserted anteriorly on cervical apodeme of pleuron. (*Retractor episterni prothoracis* Morison; *prothoracic furco-pleural muscle* Duncan.) The muscles of this pair cannot be retractors of the episterna because of the endosternal attachments of the pleura.

52. *Intersegmental ventral muscle of the prothorax; endosternal retractor of the propectus* (fig. 12 C).—A slender muscle attached anteriorly on base of proendosternum, posteriorly on supraneural bridge of mesoendosternum (fig. 22 C). (*Retractor prothoracis* Morison; *first furcal retractor of the propectus* Duncan, the second retractor of *Vesputula* absent in *Apis*.)

53. *Lateral promotor of the fore coxa* (fig. 13 C, D, G).—A broad muscle arising on episternum, inserted laterally on coxa anterior to pleural articulation.

54. *Mesal promotor of the fore coxa* (fig. 13 C, D).—A small muscle arising on side of endosternum, inserted on anterior mesal angle of coxal base.

55. *First lateral remotor of the fore coxa* (figs. 12 C, 13 C, D, G).—Longest of the coxal muscles, arises laterally on pronotum at base of spiracular lobe (fig. 17 C), inserted on outer rim of coxa behind pleural articulation.

56. *Second lateral remotor of the fore coxa* (figs. 11 C, 12 C, 13 C, D, G).—A large muscle arising on under surface of supraneural bridge of endosternum (figs. 11 C, 12 C), inserted on margin of coxal base close behind 55 (fig. 13 D, G).

57. *Mesal remotor of the fore coxa* (figs. 11 C, 13 C, D).—Smallest of the coxal muscles, arising on upper end of pleural apophysis (fig. 11 C), inserted mesally on posterior edge of coxal base (fig. 13 C, D).

58. *Coxal retractor of the propectus* (figs. 11 C, 12 C, 13 C, D, G).—A large muscle arising posteriorly on anterior part of median ridge of pterothoracic endosternum (fig. 22 C), the pair diverging forward to insertions on fore coxae mesad of pleural articulations (fig. 13 C, D). (*Extensor coxae prothoracis* Morison; *mesosternal retractor of the propectus* Duncan.)

59. *Anterior levator of the fore trochanter* (fig. 13 E, H).—Origin in coxa, inserted anteriorly on base of trochanter beyond coxal articulation.

60. *Posterior levator of the fore trochanter* (fig. 13 E, H).—Origin in coxa, inserted posteriorly on base of trochanter beyond coxal articulation. Morison mentions only one trochanteral levator, but two are present in both the drone and the worker.



61. *Thoracic depressor of the fore trochanter* (figs. 11 C, 12 C, 13 D, E, H).—A long muscle with origin on pleural apophysis of prothorax (not on endosternum as stated by Morison), going downward into coxa where fibers inserted on depressor apodeme of trochanter.

62. *Coxal depressor of the fore trochanter* (fig. 13 E, H).—A broad muscle occupying entire mesal wall of coxa, fibers inserted on depressor apodeme and apodemal plate of trochanter (fig. 13 E).

63. *Reductor of the fore femur* (fig. 13 H).—A short broad muscle arising on anterior wall of trochanter, inserted somewhat ventrally on posterior margin of base of femur.

64. *Extensor of the fore tibia*.—Origin dorsally in femur, inserted dorsally on base of tibia.

65. *Flexor of the fore tibia*.—Origin ventrally in femur, inserted on ventral genuflexor plate at base of tibia.

66. *Productor of the fore tarsus* (fig. 14 E).—A flat muscle arising on anterior wall of tibia, inserted anteriorly on base of tarsus.

67. *Reductor of the fore tarsus* (fig. 14 E).—A flat muscle arising on posterior wall of tibia, inserted posteriorly on base of tarsus.

68. *Depressor of the fore tarsus* (fig. 14 D, E).—A longer muscle than the last two, arising ventrally in tibia, inserted ventrally on base of tarsus.

69. *Flexor of the pretarsal claws of the fore leg*.—Fibers in two groups arising one in femur, the other in tibia, inserted on long slender tendon traversing tarsus, tibia, and femur from attachment at base of unguitractor plate of pretarsus.

70. *External longitudinal dorsal muscle of the mesothorax* (fig. 16 D).—A small submedian muscle traversing the mesocutellum.

71. *Internal longitudinal dorsal muscle of the mesothorax; indirect depressor of the wing* (fig. 16 A, C).—A huge muscle attached anteriorly on prephragma of mesonotum and on median area (fig. 16 B) of scutum, attached posteriorly on postphragma of mesonotum.

72. *Tergosternal muscle of the mesothorax; indirect elevator of the wing* (fig. 16 A, C).—A thick column of fibers attached dorsally on lateral area of mesoscutum (fig. 16 B), attached ventrally on sternal area of pleurosternal region.

73. *Occlusor of the first spiracle* (fig. 17 C, F).—A slender muscle arising on anterior margin of mesepisternum (C), inserted in spiracular membrane in front of spiracular aperture (F).

74. *Pleuroalar muscle of the mesothorax* (fig. 19 C).—A small, two-branched muscle arising on anterior margin of mesepisternum

(fig. 17 C), inserted on ventral side of humeral complex of first wing (fig. 19 C).

75. *Pleurotergal muscle of the mesothorax* (fig. 17 E).—A large, fan-shaped muscle arising on episternum, the fibers convergent to short tendon attached on lateral margin of posterolateral plate of scutum (fig. 19 F). (*Retractor scutelli mesothoracis* Morison.)

76. *Pleuroaxillary muscles of the mesothorax; flexors of the fore wing* (figs. 17 E, 19 H).—Three small muscles arising on mesopleuron, inserted by separate tendons on third axillary of wing base.

77. *Basalar muscle of the mesothorax* (figs. 17 E, 19 G).—A broad muscle with spreading fibers arising ventrally on anterior part of episternum, inserted dorsally by strong tendon on basalar sclerite.

78. *Muscle of the axillary lever of the mesothorax* (fig. 20 A, B).—Origin by broad base ventrally on mesothoracic arm of pterothoracic endosternum, insertion dorsally on end of lever sclerite of fourth axillary. (*Musculus furco-lateralis mesothoracis* Morison.) In non-apoid Hymenoptera this muscle is a muscle of the postphragma (fig. 20 C to H).

79. *Pleurosternal muscle of the mesothorax* (fig. 17 G).—A mass of short fibers arising on posterior epimeral area and on pleural apophysis of mesothorax, attached on end of mesothoracic arm of pterothoracic endosternum.

80. *Lateral promotor of the middle coxa* (figs. 17 G, 22 C).—A slender muscle arising on the small pleural apophysis of mesopleuron, inserted laterally on coxal base anterior to pleural articulation.

81. *Mesal promotor of the middle coxa* (fig. 22 C).—Smallest of the mesocoxal muscles, arising on basal plate of endosternum, inserted mesally on anterior margin of coxa.

82. *Lateral remotor of the middle coxa; coxosubalar muscle of the mesothorax* (figs. 17 G, 22 C).—A long muscle attached ventrally on base of coxa just posterior to pleural articulation, attached dorsally by long tendon on subalar sclerite. Probably has little motor effect on the coxa; deflects the wing posteriorly by indirect tension on the third axillary. (*Flexor coxae mesothoracis* Morison; no corresponding muscle given by Duncan in mesothorax of the wasp.)

83. *Mesal remotor of the middle coxa* (fig. 22 C).—Largest of the coxal muscles, origin on basal plate of endosternum, insertion mesally on posterior margin of base of coxa.

84. *Anterior levator of the middle trochanter* (fig. 22 D).—Origin in lower part of coxa, insertion anteriorly on base of trochanter beyond coxal articulation.

85. *Posterior levator of the middle trochanter* (fig. 22 D).—Origin posteriorly in coxa, insertion posteriorly on base of trochanter beyond coxal articulation.

86. *Thoracic depressor of the middle trochanter* (fig. 22 C, G).—Origin dorsally on side of endosternum (C), insertion on end of depressor apodeme of trochanter (G).

87. *Anterior coxal depressor of the middle trochanter* (fig. 22 D, G).—Origin anteriorly in base of coxa (D), insertion on base of depressor apodeme of trochanter (G).

88. *Posterior coxal depressor of the middle trochanter* (fig. 22 D, G).—Origin posteriorly in base of coxa (D), insertion on base of depressor apodeme of trochanter (G).

89. *Reductor of the middle femur* (fig. 22 D, G).—Origin antero-dorsally in trochanter, insertion posteroventrally on base of femur.

90. *Extensor of the middle tibia* (fig. 22 L).—A long pinnate muscle arising on dorsal wall of femur, inserted by axial tendon on dorsal process of base of tibia.

91. *Flexor of the middle tibia* (fig. 22 J).—A muscle similar to but larger than the extensor, arising on ventral wall of femur, inserted by its tendon on ventral genuflexor plate (*gf*) at base of tibia.

92. *Productor of the middle tarsus* (fig. 22 E).—A slender pinnate muscle arising anteriorly in tibia, inserted by tendon anteriorly on base of tarsus.

93. *Reductor of the middle tarsus* (fig. 22 E).—Similar to the producter, arising posteriorly in tibia, inserted posteriorly on base of tarsus.

94. *Depressor of the middle tarsus* (fig. 22 F).—A broad pinnate muscle arising on ventral wall of tibia, inserted ventrally on base of tarsus.

95. *Flexor of the pretarsal claws of the middle leg*.—Same as in fore leg and hind leg, one group of fibers arising in base of femur, another in tibia, inserted by long tendon on unguitractor plate at base of pretarsus.

96. *Retractor of the mesothoracic postphragma* (figs. 16 C, 27 C).—A small fan-shaped muscle arising by narrow end on posterior median process of propodeum, fibers spreading anteriorly and laterally to attachments on side of postphragma of mesothorax. (*Musculus retractor mesophragmati* Morison, *mesophragma retractor muscle* Betts.) The muscles of this pair probably are the longitudinal dorsal muscles of the metathorax with their propodeal attachments shifted posteriorly.

97. *First tergosternal muscle of the metathorax* (fig. 21 F, G).—Origin by broad base on metathoracic arm of endosternum, insertion on anterior angle of lateral plate of metanotum (E).

98. *Second tergosternal muscle of the metathorax* (fig. 21 F, G).—Origin on metathoracic endosternal arm posterior to 97, insertion on posterior angle of lateral notal plate (E).

99. *Third tergosternal muscle of the metathorax* (fig. 21 F).—Attached ventrally by narrowed end on small tongue (*c*) of metathoracic arm of endosternum, fibers spreading dorsally to triangular lateral area of metanotum.

100. *Pleuroaxillary muscle of the metathorax; flexor of the hind wing* (fig. 21 B, H).—A small, three-part, fan-shaped muscle arising on anterior marginal inflection of metapleuron, fibers converging to small nodule in membrane of wing base (*a*) close to third axillary.

101. *Basalar muscle of the metathorax* (fig. 21 H).—A large muscle arising by broad base on apodemal lobe of metathorax behind meso-coxal cavity (fig. 16 H, *r*), inserted dorsally by a strong tendon on basalar sclerite (fig. 21 B).

102. *Pleurosubalar muscle of the metathorax* (fig. 21 C, H).—A broad, thick, fan-shaped muscle arising on metapleuron, fibers convergent to narrow insertion on subalar sclerite. (Not given by Morison; two corresponding muscles in *Vespula*, Duncan.)

103. *Lateral promotor of the hind coxa* (fig. 24 A, B).—A fan-shaped muscle arising on ridge between mesopleuron and propodeum, the convergent fibers inserted laterally on anterior margin of coxa.

104. *Mesal promotor of the hind coxa* (fig. 24 A, B).—Origin on metasternal component of pterothoracic endosternum, insertion mesally on anterior coxal margin.

105. *Lateral remotor of the hind coxa; coxosubalar muscle of the metathorax* (fig. 24 A, B).—A long muscle attached below on coxa immediately behind pleural articulation, inserted dorsally by long tendon on apodeme of subalar sclerite (fig. 21 B, C). Deflects the wing posteriorly. (Wrongly said by Morison to arise on endosternum.)

106. *Mesal remotor of the hind coxa* (fig. 24 A, B).—Origin by wide base on metasternal component of pterothoracic endosternum, inserted by broad tendon in articular membrane close to posterior mesal angle of base of coxa.

107. *Anterior levator of the hind trochanter* (fig. 24 C, D).—Origin anteriorly in coxa, insertion by tendon in dorsal membrane of coxo-trochanteral joint beyond anterior coxal articulation (D).



108. *Posterior levator of the hind trochanter* (fig. 24 C, D).—Origin posteriorly in coxa, insertion in dorsal membrane of coxo-trochanteral joint beyond posterior coxal articulation (D).

109. *Thoracic depressor of the hind trochanter* (fig. 24 A, C).—Origin on metathoracic arm of pterothoracic endosternum (A), fibers convergent into coxa to insertion on long depressor apodeme of trochanter (D, *Ap*).

110. *Coxal depressor of the hind trochanter* (fig. 24 C, E).—A broad muscle arising ventrally in coxa, the convergent fibers inserted on base of depressor apodeme of trochanter (E).

111. *Reductor of the hind femur* (fig. 24 C).—A short thick muscle arising anterodorsally in trochanter, inserted ventroposteriorly on apodemal inflection of base of trochanter (F, *Ap*).

112. *Extensor of the hind tibia* (fig. 24 H).—A long pinnate muscle arising along dorsal wall of femur, inserted by tendon on dorsal knob of base of tibia.

113. *Flexor of the hind tibia* (fig. 24 H).—A large pinnate muscle lying in ventral half of tibia, fibers attached anteriorly and posteriorly, inserted by strong axial tendon on ventral genuflexor plate at base of tibia (G, H, *gf*).

114. *Promotor of the hind tarsus* (fig. 24 J, K, L).—Origin ventrally on anterior wall of wide distal part of tibia (K, L), inserted anteriorly on base of tarsus (J).

115. *Levator of the hind tarsus* (fig. 24 J, K, L).—A fan-shaped muscle arising on posterior wall of distal part of tibia (K), inserted posteriorly by narrow stalk on base of tarsus but above level of tibial articulation (J). Corresponds with the reductor of the other legs.

116. *Depressor of the hind tarsus* (fig. 24 J, K, L).—Much larger than the other two tarsal muscles, arises on anterior wall of tibia (K), inserted ventrally on base of tarsus (J, L).

117. *Flexor of the pretarsal claws of the hind leg* (fig. 24 H, K).—As in the other legs, a two-branched muscle, one branch arising posteriorly in base of femur (H, 117*a*), the other posteriorly in base of tibia (K, 117*b*), both branches inserted on long apodemal tendon extending through tarsus and tibia into femur from its origin in articular membrane at base of unguitractor plate of pretarsus, as in middle leg (fig. 25 B, 95*Ap*).

118. *Median intersegmental ventral muscle of the metathorax; median depressor of the abdomen* (fig. 27 E).—A long muscle arising anteriorly on metasternal component of pterothoracic endosternum, inserted posteriorly by broad tendon medially on sternum of petiole segment (118).



119. *Lateral intersegmental ventral muscle of the metathorax; ventral latcromotor of the abdomen* (fig. 27 E).—A smaller muscle arising on median ridge of metasternum (in drone), inserted by long tendon laterally on sternum of petiole segment (IIS).

120. *Outer dorsal muscle of the propodeum; median levator of the abdomen* (fig. 27 B).—A large muscle with spreading fibers arising on lateral wall of propodeum, inserted by strong tendon on median ridge of pocket on dorsal side of petiole (D, F, G). (*Petiole muscle* Betts; *musculus propodei retractor dorsalis postabdominis* Morison.)

121. *Inner dorsal muscle of the propodeum; dorsal lateromotor of the abdomen* (fig. 27 B).—A two-branched muscle arising laterally on propodeum at base of 120, inserted by long thick tendon on lateral angle of tergal plate of petiole (G).

122. *Occluser of the propodeal spiracle* (fig. 27 B).—A short intraspiracular muscle.

123. *Dilator of the propodeal spiracle* (fig. 27 B).—A long slender muscle arising from small process on dorsal margin of hind coxal cavity.

124. *Median internal dorsal muscle of abdominal segment II* (fig. 28 A).

125. *Lateral internal dorsal muscle of abdominal segment II* (fig. 28 A).

126. *External dorsal muscle of abdominal segment II* (fig. 28 A).—Runs transversely in fold between tergum II and tergum III.

127. *Occluser of the spiracle of abdominal segment II*.—A short intraspiracular muscle.

128. *Dilator of the spiracle of abdominal segment II* (fig. 28 A).—A long slender muscle arising ventrally on lateral margin of sternum II.

129. *Lateral muscle of abdominal segment II* (fig. 28 A).—The only tergo-sternal muscle of segment II, being attached on dorsal surface of sternum it is probably the third lateral of other segments.

130. *Median internal ventral muscle of abdominal segment II* (fig. 28 A).—The only internal ventral muscle in segment II of the female.

131. *Lateral internal ventral muscle of abdominal segment II* (fig. 29 B).—Present in the male only.

132. *External ventral muscle of abdominal segment II* (fig. 28 A).—Runs transversely from posterior part of sternum II to anterior apodeme of sternum III.

The muscles of the next four abdominal segments are repeated alike in each of these segments, and are present in both the male and the female; they are numbered in the female (fig. 28 A), and may

easily be identified by comparison in the male (fig. 29 B), though the muscles of the male are much larger and the second and third laterals are not crossed.

133, 144, 155, 166. *Median internal dorsal muscles of abdominal segments III to VI* (fig. 28 A).

134, 145, 156, 167. *Lateral internal dorsal muscles of abdominal segments III to VI* (fig. 28 A).

135, 146, 157, 168. *External dorsal muscles of abdominal segments III to VI* (fig. 28 A).—Oblique in anterior segments, reversed in posterior segments; origins posteriorly on anterior tergum, insertion anterior on anterior apodeme of posterior tergum.

136, 147, 158, 169. *Occlusors of the spiracles of abdominal segments III to VI* (not shown in figures).

137, 148, 159, 170. *Dilators of the spiracles of abdominal segments III to VI* (fig. 28 A).—Origins on long lateral apodemes of the sterna.

138, 149, 160, 171. *First lateral muscles of abdominal segments III to VI* (figs. 26 D, 28 A).—Reversed tergoventral muscles arising ventrally on lower parts of terga, inserted dorsally on lateral apodemes of corresponding sterna.

139, 150, 161, 172. *Second lateral muscles of abdominal segments III to VI* (fig. 28 A).—External tergoventral muscles attached ventrally on lateral margins of the sterna; dorsoventral in the male (figs. 26 E, 29 B), oblique in the female (fig. 28 A).

140, 151, 162, 173. *Third lateral muscles of abdominal segments III to VI* (fig. 28 A).—Internal tergoventral muscles attached ventrally in posterolateral angles of dorsal surfaces of sternal plates (fig. 26 E), parallel with second laterals in the male (figs. 26 E, 29 B), crossing the latter obliquely in the female (fig. 28 A).

141, 152, 163, 174. *Median internal ventral muscles of abdominal segments III to VI* (fig. 28 A, B).—In each segment the median ventrals form a V with the convergent ends posterior (B); in the male these muscles are wide bands of fibers.

142, 153, 164, 175. *Lateral internal ventral muscles of abdominal segments III to VI* (fig. 28 A, B).—The lateral ventrals are oblique in an opposite direction from the median ventrals, the two sets forming in each segment an M.

143, 154, 165, 176. *External ventral muscles of abdominal segments III to VI* (fig. 28 A).—Short reversed muscles from posterior parts of sterna to under surfaces of anterior apodemes of preceding sterna.

The musculature of abdominal segments VII to IX is unlike in the two sexes, in some cases also between queen and worker, and differs from that of the preceding segments by the absence of certain muscles

and the presence of special muscles in connection with the ovipositor and the male genital organ.

177. *Lateral internal dorsal muscle of abdominal segment VII.*—In the drone (fig. 29 B) as in preceding segments; in the queen (fig. 28 E) attached on anterior part of spiracular plate of segment VIII; absent in the worker (C).

178. *Median internal dorsal muscle of abdominal segment VII.*—In the drone (fig. 29 B) as in preceding segments; in the queen (fig. 28 E) a small muscle attached on spiracular plate of segment VIII near spiracle; in the worker (fig. 28 C) a much larger muscle similarly attached.

179. *External dorsal muscle of abdominal segment VII.*—As in preceding segments in the drone; in the female a reversed dorso-ventral muscle from lower edge of tergum VII to upper angle of spiracular plate of segment VIII (fig. 28 C, E).

180, 181. *Spiracular muscles of abdominal segment VII* (fig. 28 C).—As in preceding segments.

182. *First and second lateral muscles of abdominal segment VII.*—First lateral present as a reversed muscle inserted dorsally on lateral apodeme of sternum VII in both the drone and the worker, but very small in the latter (No. 5b of Rietschel, 1937). The muscle designated 182 in the worker (fig. 28 C) also is attached on the lateral apodeme of sternum VII, but arises posteriorly on the tergum and is probably the second lateral of segment VII.

183. *Third lateral muscle of abdominal segment VII* (fig. 28 C).—Present in both the male and the female as a dorsoventral muscle between tergum and sternum.

184. *Intersegmental sternotergal muscle of abdominal segment VII* (fig. 28 B, C).—Present in the female only; origin anteriorly on sternum VII in line with lateral ventral muscles of preceding segments (B), inserted posteriorly on anterior ventral angle of spiracular plate of segment VIII.

185. *Median internal ventral muscle of abdominal segment VII* (fig. 28 D).—Present in the queen only, attached posteriorly on lateral genital pouch.

186. *Lateral internal ventral muscle of abdominal segment VII* (fig. 29 B, D).—Present in the male only; a short muscle arising on sternum VII at base of anterior apodeme (B), inserted posteriorly on long lateral arm of sternum VIII.

187. *Median internal dorsal muscle of abdominal segment VIII.*—A short muscle in the male (fig. 29 B) attached posteriorly on apodeme of small tergite of segment IX; represented in the worker (fig. 28 C)

and the queen (E) by a muscle (187) from spiracular plate of segment *VIII* to quadrate tergal plate of segment *IX*.

188. *Lateral internal dorsal muscle of abdominal segment VIII*.—Absent in the male, perhaps represented in the worker (fig. 28 C) and the queen (E) by a muscle (188) from upper angle of spiracular plate to posterior dorsal angle of quadrate plate of segment *IX* (fig. 31 B).

189. *Occlusor of the spiracle of abdominal segment VIII* (fig. 28 C, E).—A short intraspiracular muscle.

190. *Dilator of the spiracle of abdominal segment VIII* (fig. 28 C, E).—In the worker and the queen the dilator of the spiracle of segment *VIII* arises in the ventral anterior angle of the tergal spiracular plate, not on the sternum as in preceding segments.

191. *Lateral muscle of abdominal segment VIII* (fig. 29 B, D).—Present in the male only, apparently represents the second tergo-sternal muscle of preceding segments.

192. *Tergovalvifer muscle of abdominal segment VIII*.—Present in the female only, arising on posterior ventral angle of spiracular plate (fig. 28 C, E), goes anteroventrally to insertion on dorsal margin of triangular plate (first valvifer) of sting (fig. 31 D).

193, 194. *Tergovaginal muscles of abdominal segment VIII*.—Two slender muscles present in the queen only, arising on anteroventral part of spiracular plate (fig. 28 E), inserted on dorsal wall of vagina (D).

195. *Lateral internal ventral muscle of abdominal segment VIII* (fig. 29 B, D).—A short muscle present in the male only, arising laterally on sternum *VIII*, inserted on lateral angle of parameral plate (*lp*).

196. *Levator of the shaft of the sting* (fig. 31 B, C).—A small muscle arising on middle of ramus of stylet, inserted on small process (C, *g*) of base of stylet bulb a short distance beyond hinge (*h*) between ramus and bulb.

197. *Depressor of the shaft of the sting* (fig. 31 B).—A large muscle arising posteriorly on oblong plate of sting, curving anteriorly and dorsally over base of stylet bulb to insertion on furcula (*Frc*). A small branch of this muscle is described by Rietschel (1937, No. 19b) as arising laterally on the oblong plate.

198. *Protractor of the lancet of the sting* (figs. 31 B, 32 C).—A large muscle of two parts attached posteriorly on outer and inner surfaces of upper, apodemal part of quadrate plate; attached anteriorly on anterior end of oblong plate at base of second ramus (*2r*). Pulls the quadrate plate forward, depresses the triangular plate, and pro-

tracts the lancet (fig. 32 G). The two parts of this muscle are anatomically two muscles, but functionally a single muscle. The upper part has mistakenly been said (Betts, Morison, and others) to be attached on the triangular plate.

199. *Retractor of the lancet of the sting* (figs. 31 B, 32 C).—A broad fan-shaped muscle arising anteriorly on quadrate plate, inserted posteriorly on upper edge of oblong plate. Pulls the quadrate plate backward, elevates the triangular plate, and retracts the lancet (fig. 32 F).

200, 201. *Muscles of the proctiger in the female* (fig. 31 B).—Two long slender muscles arising on posterior dorsal angle of the quadrate plate (tergite of segment IX), inserted laterally and ventrally on lower wall of proctiger.

202. *Median dorsal muscle of abdominal segment IX in the male* (fig. 29 B).—A short muscle from apodeme of small tergite of segment IX to side of proctiger. This muscle falls in line with the median dorsals of the preceding segments, and probably is represented by muscles 200 and 201 in the female.

203, 204. *Phallic muscles of the male* (fig. 29 D).—Two small muscles, or divergent parts of one muscle, arising ventrally on parameral plate (*lp*), inserted dorsally on end of apodeme of penis valve (*pv*).

205. *Muscle of the mucus gland of the male* (fig. 29 D).—A slender muscle from apodeme of penis valve to mucus gland just laterad of end of vas deferens.

#### ABBREVIATIONS USED ON THE FIGURES

*A*, anal vein.

*Ac*, antecosta.

*af*, antennafer.

*An*, anus.

*ANP*, anterior notal wing process.

*Ant*, antenna.

*Ap* or *ap*, apodeme.

*apa*, apodeme of aedeagus.

*Ar*, arolium.

*arc*, arcus

*at*, anterior tentorial pit.

*AT*, anterior tentorial arm.

*au*, auricle.

*aux*, auxilia.

*Ax*, axillary sclerite of wing base (*1Ax*, *2Ax*, *3Ax*, *4Ax*, first, second, third, and fourth axillaries).

*AxC*, axillary cord.

*axlv*, axillary lever.



- Ba*, basalaré.  
*bc*, bursal cornua, pneumapophysis.  
*BGld*, "alkaline" gland of sting.  
*bib*, biblike suboral flap.  
*blb*, bulb of sting.  
*Blb*, bulb of endophallus.  
*Br*, brain.  
*Brs*, bursa of endophallus.  
*Bs*, basisternum.  
*Btar*, basitarsus.
- C*, costa, marginal vein of wing.  
*Ca*, corpus allatum.  
*Cb*, cibarium (suctorium of cibario-pharyngeal pump).  
*cbl*, pollen basket (corbicula) of hind tibia.  
*Cc*, corpus cardiacum.  
*Cer*, neck of endophallus.  
*Cd*, cardo.  
*Clp*, clypeus.  
*cnj*, conjunctiva.  
*Cvx*, neck, cervix.  
*Cx*, coxa.  
*CxC*, coxal cavity (where coxa removed from body).  
*CxP*, pleural coxal process.
- Dej*, ductus ejaculatorius.  
*dlcb*, dilator muscles of cibarium.  
*dlphy*, dilator muscles of pharynx.  
*DT*, dorsal arm of tentorium.
- E*, compound eye.  
*Endst*, endosternum.  
*Enph*, endophallus.  
*Ephy*, epipharynx.  
*Epm*, epimeron (*cpm*, subdivision of epimeron).  
*Eps*, episternum.  
*ER*, epistomal ridge.  
*es*, sulcus of epistomal ridge (epistomal "suture").
- Fbl*, flabellum.  
*fc*, food canal of proboscis.  
*FC*, food channel on base of proboscis.  
*Fl*, flagellum.  
*flb*, fimbriate lobe of endophallus.  
*Fm*, femur.  
*For*, foramen magnum.  
*Fr*, frons.  
*Frc*, furcula.  
*FrGng*, frontal ganglion.  
*Fs*, furcasternum.

*Ga*, galea.

*Gc*, gena.

*gf*, genuflexor plate.

*Gls*, labial tongue (glossae).

*H*, head.

*HB*, hypostomal bridge.

*Hphy*, hypopharynx.

*IbS*, infrabuccal sac.

*IS*, sternal plate of propodeum.

*IT*, tergal plate of propodeum.

*IX.V*, venter of ninth abdominal segment.

*L*, leg.

*Lb*, labium.

*LbPlp*, labial palpus.

*Lc*, lacinia.

*lcl*, lacinial lobe.

*Lct*, lancet (first valvula).

*Lm*, labrum.

*lO*, lateral ocellus.

*lp*, lamina parameralis.

*Lr*, lorum.

*Lsp*, lamina spiracularis (tergite of eighth abdominal segment).

*lvr*, lever of lacinia.

*Mb*, intersegmental membrane.

*MCu*, mediocubital vein.

*Md*, mandible.

*MdC*, cavity where mandible removed from head.

*MdGld*, mandibular gland.

*mn*, manubrium of arolium.

*mO*, median ocellus.

*Mth*, mouth.

*Mx*, maxilla.

*MxPlp*, maxillary palpus.

*N*, notum (thoracic tergum).

*nf*, neural foramen.

*NR*, notal ridge.

*ns*, sulcus of notal ridge (scutoscuteellar "suture").

*Nv*, nerve.

*O*, ocellus.

*Ob*, oblong plate of sting (second valvifer).

*Oc*, occiput.

*occ*, occipital condyle.

*Odc*, oviductus communis.

*Odl*, oviductus lateralis.

*Oe*, oesophagus.

*Op*, operculum of first spiracle.

*opl*, oral plate.

*pc*, poison canal of sting.

*Pdc*, pedicel of antennal flagellum.

*PF*, proboscis fossa.

*Pge*, postgena.

*Pgl*, paraglossa.

*PgL*, postgenal lobe.

*Ph*, phragma (*1Ph*, first phragma, *2Ph*, second phragma).

*Phtr*, phallotreme.

*Phy*, pharynx.

*Pl*, pleuron (*pl*, subdivision of pleuron).

*pla*, pit of pleural apophysis.

*PLA*, pleural apophysis.

*Plf*, palpifer.

*Plg*, palpiger.

*pln*, planta.

*Plp*, palpus.

*PlR*, pleural ridge.

*pls*, sulcus of pleural ridge (pleural "suture").

*Pmr*, paramere.

*Pmt*, postmentum.

*PN*, postnotum.

*Poc*, postocciput.

*pos*, postoccipital suture.

*pr*, pollen press.

*Prb*, proboscis.

*Prmt*, prementum.

*PsnSc*, poison sack.

*pt*, posterior tentorial pit.

*Ptar*, pretarsus.

*Ptgr*, proctiger.

*pv*, penis valve (lamina aedeagalis).

*Qd*, quadrate plate of sting (tergite of ninth abdominal segment).

*r*, ramus of sting (*1r*, ramus of lancet; *2r*, ramus of stylet).

*R*, radius.

*ras*, rastellum.

*rd*, glossal rod.

*Rdp*, reduplication of posterior margin of notum.

*RNv*, recurrent nerve.

*S*, sternum.

*Sa*, subalare.

*SA*, sternal apophysis.

*sc*, salivary canal of tongue.

*Scl*, scutellum.

- Scp*, scape.  
*Sct*, scutum (*sct*, subdivision of scutum).  
*sf*, scutal fissure (trans-scutal "suture").  
*Sga*, subgalea.  
*Sh*, sheath lobe of sting.  
*SID*, salivary duct.  
*SIO*, salivary orifice.  
*Slv*, salivarium (salivary syringe).  
*Sp*, spiracle.  
*spl*, spiracular lobe of pronotum.  
*spmb*, spiracular membrane.  
*SptD*, spermathecal duct.  
*St*, stipes.  
*Stl*, stylet (united second valvulae).  
*Syr*, salivary syringe.
- T*, tergum.  
*Tar*, tarsus.  
*Tb*, tibia.  
*TB*, tentorial bridge.  
*Tg*, tegula.  
*Tr*, trochanter.  
*Tra*, trachea.  
*Tri*, triangular plate of sting (first valvifer).
- Un*, unguis (lateral claw of pretarsus).  
*Utr*, unguitractor plate.
- V*, venter.  
*VDph*, ventral diaphragm.  
*Vlv*, valve on lancet.
- W*, wing.  
*WP*, pleural wing process.

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## A REVISION OF THE INDO-CHINESE FORMS OF THE AVIAN GENUS PRINIA

By H. G. DEIGNAN

*Associate Curator, Division of Birds, U. S. National Museum*

One using the "Fauna of British India, Birds," 2d edition, can scarcely fail to be astonished by the unnatural classification employed in certain families in consequence of Stuart Baker's use in a generic, or even subfamilial, sense of characters which, in themselves, are, at most, of not more than subspecific importance. The pitfalls into which such false evaluation may lead are nowhere more evident than in his treatment of the Sylviidae, where, merely on a basis of whether the species have 10 or 12 rectrices, we find *Phyllergates* separated from *Orthotomus* by 21 genera, while *Prinia* is divided from *Franklinia* by 23 and from *Cisticola* by 24 genera. In the case of *Franklinia*, one can find not a single character of generic importance by which the putative genus may be upheld as distinct from *Prinia* and, once the principle is accepted that the number of tail feathers may be related to geographical variation within the species (as it is, indeed, generally accepted in the cases of certain African warbler species), one hesitates to accept even the specific distinctness of the Indian *Prinia socialis* from the Indo-Chinese *Franklinia rufescens*. As for the so-called genus *Suya*, which has not one character by which it may be distinguished from *Prinia*, it is hardly necessary to say more than that the form called *Suya crinigera cooki* is only with difficulty differentiated subspecifically from the Javanese bird accepted by all modern authors as *Prinia polychroa*. The seasonal change in tail length, assumed by Baker to have generic importance in *Prinia*, *Suya*, *Franklinia*, and *Laticilla*, is reduced to its proper insignificance by the realization that such variation gradually disappears, from north to south, even within the limits of the several species as conceived by Baker himself. In short, the genus *Prinia*, in this paper, is considered to be a poorly defined aggregation of grass warblers, nearly allied (through *Incana*) to those placed by Lynes in *Cisticola* and, in Asia, embracing all the forms distributed by Baker among *Prinia*, *Suya*, *Laticilla*, and *Franklinia*.

The present study has been inspired and facilitated by the valuable contributions to an understanding of the Indian *Prinia* made by Whistler and Kinnear<sup>1</sup> and by Ticehurst and Whistler.<sup>2</sup>

For the loan of long series of specimens to be added to those in the collection of the United States National Museum (U.S.N.M.) and without which the work would not have been possible, I am indebted to the authorities of the Academy of Natural Sciences of Philadelphia (A.N.S.), of the American Museum of Natural History (A.M.N.H.), of the Museum of Comparative Zoology (M.C.Z.) and of the Princeton Museum of Zoology (P.M.Z.).

## I

The Indo-Chinese populations of *Prinia rufescens*, hitherto submerged in *Franklinia rufescens* (Blyth), prove, upon examination of series in comparable plumages, to fall into no fewer than five well-characterized races, localized in just those areas where subspecific differentiation normally appears in numerous other passerine species.

### 1. PRINIA RUFESCENS RUFESCENS Blyth

*Pr[inia] rufescens* BLYTH, Journ. Asiat. Soc. Bengal, vol. 16, p. 456, 1847 (Arakan).

Front, crown, and nape brownish slate (summer); rufous brown, tinged with slate (winter).

Mantle dark rufous brown (summer); bright rufous brown (winter).

Well-marked supraloral streak (often continued beyond the eye as a short supercilium) and the tiny feathers of both eyelids white (summer and winter).

Under parts white, washed with buff, most strongly along the flanks and on the thighs and under tail-coverts (summer); white, washed with rufous buff, most strongly along the flanks, over the greater part of the abdomen, and on the thighs and under tail-coverts (winter).

Tail short in summer, slightly longer in winter.

*Range*.—In Indo-China (excepting Burma): the northern half of Indochine; East Siam, south to the river Me Mu'n (U:bon Province); all North Siam; West Siam, south to lat. 14° N.

Walden has named *Prinia beavani* from two examples collected at Shwegun, Salwin River, Tenasserim (Proc. Zool. Soc. London, 1866

<sup>1</sup> Journ. Bombay Nat. Hist. Soc., vol. 36, pp. 564-566, 573-582, 1933.

<sup>2</sup> Ibis, 1939, pp. 761-763.



[=1867], p. 551); I find no points of difference between the birds of northern Tenasserim and those of other parts of southern Burma and unqualifiedly pronounce *beavani* synonymous with *rufescens*.

## 2. PRINIA RUFESCENS PENINSULARIS, new subspecies

*Type*.—Adult female, U.S.N.M. No. 160572, collected at Trang, Peninsular Siam, January 20, 1897, by W. L. Abbott.

Front, crown, and nape brownish slate (summer); brownish slate or slaty brown (winter).

Mantle dark rufous brown (summer and winter).

Well-marked supraloral streak (often continued beyond the eye as a short supercilium) and the tiny feathers of both eyelids white (summer and winter).

Under parts white, washed with buff, most strongly along the flanks and on the thighs and under tail-coverts (summer and winter).

Tail short (summer and winter).

*Range*.—Peninsular Siam, from the Isthmus of Kra: south to (but not including) Pattani Province.

## 3. PRINIA RUFESCENS EXTREMA, new subspecies

*Type*.—Adult male, U.S.N.M. No. 308245, collected at Bangna:ra, Peninsular Siam, July 13, 1926, by H. M. Smith.

Front, crown, and nape dark brownish slate (summer and winter).

Mantle dark rufescent olivaceous brown (summer and winter).

Well-marked supraloral streak white (summer and winter).

Tiny feathers of upper eyelid white, those of lower eyelid mixed white and slaty (summer and winter).

Under parts white, washed with pale buff, most strongly along the flanks and on the thighs and under tail-coverts (summer and winter).

Tail short (summer and winter).

*Range*.—Peninsular Siam (Pattani Province) and the Malay States, south to Negri Sembilan and Pahang.

## 4. PRINIA RUFESCENS OBJURGANS, new subspecies

*Type*.—Adult male, U.S.N.M. No. 334623, collected at Siracha, southeastern Siam, April 19, 1934, by H. M. Smith.

Front, crown, and nape brownish slate (summer and winter).

Mantle dark rufous brown (summer and winter).

Well-marked supraloral streak white (summer and winter).

Tiny feathers of upper eyelid mixed white and slaty, those of lower eyelid slaty (summer and winter).

Under parts white, washed with buffy cream, most strongly along the flanks and on the thighs and under tail-coverts (summer and winter).

Tail short (summer and winter).

Range.—Southeastern Siam.

#### 5. *PRINIA RUFESCENS DALATENSIS* (Riley)

*Franklinia rufescens dalatensis* RILEY, Proc. Biol. Soc. Washington, vol. 53, p. 79, 1940 (Fimnon, South Annam).

Front, crown, and nape dark brownish slate (summer); dark rufous brown, tinged with slaty (winter).

Mantle dark rufous brown (summer and winter).

Indistinct supraloral streak slaty or mixed white and slaty (summer and winter).

Tiny feathers of both eyelids slaty (summer and winter).

Under parts white, washed with buffy rufous, most strongly along the flanks and on the thighs and under tail-coverts (summer and winter).

Tail short in summer, slightly longer in winter.

Range.—South Annam.

I am tempted to consider *Prinia rufescens* and its races merely the more eastern forms of the species named *Pr. socialis* by Sykes. Judging by the literature, however, there seems to be considerable overlapping of ranges in the eastern Himalayas and Assam and, assuming that such overlapping is real, rather than merely apparent, I keep them, at least for the present, distinct specific entities.

## II

With the inclusion of the genus *Franklinia* Jerdon 1863 in *Prinia* Horsfield 1821, *Prinia gracilis* Franklin 1831 is preoccupied by *Sylvia* [= *Prinia*] *gracilis* Lichtenstein 1823 and Blyth's *Pr[inia] Hodgsonii* again comes into use for the bird of Central India, thus becoming untenable for the Himalayan race, which may be called *Prinia hodgsonii rufula* Godwin-Austen 1874.

Of *Prinia hodgsonii*, I find at least four forms in the Indo-Chinese countries.

#### 1. *PRINIA HODGSONII HODGSONII* Blyth

*Pr[inia] Hodgsonii* BLYTH, Journ. Asiat. Soc. Bengal, vol. 13, p. 376, 1844.

New name for *Prinia gracilis* Franklin 1831 (Mirzapur District, by restriction, Ticehurst and Whistler, Ibis, 1939, p. 763), not *Sylvia gracilis* Lichtenstein 1823.

Upper parts nearest hair brown (Ridgway), this color almost pure on front, crown, and nape, faintly tinged rufescent on mantle, rump, and upper tail-coverts (summer); light olivaceous brown, suffused with rufescent, faintly on front, crown, and nape, more strongly on mantle, conspicuously on rump and upper tail-coverts (winter).

Supraloral streak ashy white (summer and winter).

The swollen edges of the eyelids orange and the tiny feathers of both eyelids white (summer); the edges of the eyelids neither swollen nor brightly colored, the tiny feathers of both eyelids white (winter).

Under parts white, with a broad pectoral band and flanks deep ashy gray, the throat and center of abdomen very faintly tinged with cream (summer); white (more or less sullied with ashy gray on breast and upper flanks), washed with cream, which posteriorly changes to light rufous cream (winter).

Tail short in summer, longer in winter.

*Range*.—In Indo-China: Burma, south of Manipur and west of the Irriwadi River.

## 2. PRINIA HODGSONII RUFULA Godwin-Austen

*Prinia rufula* GODWIN-AUSTEN, Proc. Zool. Soc. London, 1874, p. 47 (Naga Hills and Manipur).

Upper parts between hair brown (Ridgway) and chætura drab (Ridgway), this color almost pure on front, crown, and nape, faintly tinged rufescent on mantle, rump, and upper tail-coverts (summer); dark olivaceous brown, suffused with rufescent, faintly on front, crown, and nape, more strongly on mantle, conspicuously on rump and upper tail-coverts (winter).

Supraloral region concolorous with crown (summer); supraloral streak ashy white (winter).

The swollen edges of the eyelids orange and the tiny feathers of both eyelids slaty (summer); the edges of the eyelids neither swollen nor brightly colored, the tiny feathers of the upper eyelid mixed ashy gray and white, those of the lower eyelid white (winter).

Under parts white, with a broad pectoral band and flanks deep ashy gray, the throat and center of abdomen washed with cream (summer); white (more or less sullied with ashy gray on breast and upper flanks), washed with cream, which posteriorly changes to light rufous cream (winter).

Tail short in summer, longer in winter.

*Range*.—In Indo-China: Upper Burma, except for those districts inhabited by *hodgsonii*.

3. *PRINIA HODGSONII CONFUSA*, new subspecies

*Type*.—Adult male, M.C.Z. No. 129216, collected at Mengtze, SE. Yunnan, December 5, 1920, by J. D. La Touche.

Upper parts chætura drab (Ridgway), this color almost pure on front, crown, and nape, faintly tinged rufescent on mantle, rump, and upper tail-coverts (summer); dark olivaceous brown, suffused with bright rufous, faintly on front, crown, and nape, strongly on the mantle, very conspicuously on the rump and upper tail-coverts (winter).

Supraloral region concolorous with crown (summer); supraloral streak ashy white (winter).

The swollen edges of the eyelids orange and the tiny feathers of both eyelids slaty (summer); edges of eyelids neither swollen nor brightly colored, the tiny feathers of the upper eyelid mixed ashy gray and white, those of the lower eyelid ashy white (winter).

Under parts white, with a broad pectoral band and flanks deep ashy gray, the throat and center of abdomen faintly washed with cream (summer); white (very slightly sullied with ashy gray on breast and upper flanks), washed with creamy rufous, faintly on throat and breast but strongly posteriorly (winter).

Tail short in summer, longer in winter.

*Range*.—Yunnan, Tongking, and adjacent parts of Laos.

In *confusa*, the northeasternmost form of *Prinia hodgsonii*, we find the greatest differentiation between summer and winter plumages and, in the latter, the strongest resemblance to the corresponding dress of a race of *Prinia rufescens* inhabiting the same area. It is evidently this approximation which puzzled Whistler and Kinnear<sup>3</sup> and which, at one time, misled Delacour into believing *hodgsonii* and *rufescens* mere color phases of a single species. Despite their similarity, however, *confusa* may readily be known from *rufescens* by a character which serves equally well to separate all other cohabitant forms of the two species: in the former, the under side of the rectrices is brownish ashy, with black subterminal spot and ashy white tip; in the latter, the under side of the rectrices is ashy brown, with black subterminal spot and rufous gray tip.

4. *PRINIA HODGSONII ERRO*, new subspecies

*Type*.—Adult female, U.S.N.M. No. 350283, collected at Chieng-mai, 1,000 feet, North Siam, January 24, 1936, by H. G. Deignan.

<sup>3</sup> Journ. Bombay Nat. Hist. Soc., vol. 36, p. 565, 1933.

Upper parts chaetura black (Ridgway), this color almost pure on front, crown, and nape, faintly tinged rufescent on mantle, rump, and upper tail-coverts (summer); front, crown, and nape slaty brown or brownish slate, changing gradually to dark olivaceous brown, suffused with rufescent on the lower back, rump, and upper tail-coverts (winter).

Supraloral region concolorous with crown (summer); supraloral streak dark ashy, very rarely ashy white (winter).

The swollen edges of the eyelids orange and the tiny feathers of both eyelids slaty (summer); the edges of the eyelids neither swollen nor brightly colored, the tiny feathers of the upper eyelid ashy gray, those of the lower eyelid ashy gray or mixed ashy gray and white (winter).

Under parts white, with a broad pectoral band and flanks deep ashy gray, the throat and center of abdomen faintly tinged with cream (summer); white (more or less sullied with ashy gray on breast and upper flanks), washed with cream, which posteriorly changes to rufous cream (winter).

Tail short (summer and winter, but occasionally longer in winter).

*Range*.—Kengtung State, North Siam, and Middle Laos.

*Prinia hodgsonii* occurs also in East and Southeast Siam and in South Annam but the material from those areas available to me is too scant to warrant expression of opinion as to subspecies.

In summer dress, all the races of *Pr. hodgsonii* are very distinct from those of *Pr. rufescens* but variation within the species appears only in the most subtle characters; in winter dress, they are easily distinguishable from each other but then show a strong, though superficial, resemblance to those of the other species.

### III

*Prinia inornata* (with which I consider the African *Drymoica superciliosa* Swainson and its races conspecific) is represented in the Indo-Chinese countries (excluding Burma) by three forms.

#### 1. PRINIA INORNATA BLANFORDI (Walden)

*Drymæca blanfordi* WALDEN, in Blyth, Cat. Mamm. Birds Burma, Journ. Asiat. Soc. Bengal, vol. 43, pt. 2, extra No., p. 118, 1875 (Toungoo, Burma).

*Range*.—In Indo-China (excepting Burma): North Siam (Chiengmai Province).

This species has been taken in northern Siam only at Chiengmai, Mu'ang Fang, and Nan. Fine-plumaged January birds from Chieng-



mai may quite safely be called *blanfordi*; a couple of worn summer specimens from Mu'ang Fang are subspecifically indeterminable; the sole example yet known from Nan is discussed below.

## 2. *PRINIA INORNATA EXTENSICAUDA* (Swinhoe)

*Drymoica extensicauda* SWINHOE, Ibis, 1860, pp. 50-51 (Amoy).

*Range*.—In Indo-China: Tongking, North Annam, High Laos.

The single worn and discolored specimen from Nan, placed by Riley<sup>4</sup> with "*exter*" because it "matches . . . perfectly" summer birds from western Szechuan, in fact agrees equally well with similar examples from Amoy (*extensicauda*) and from Mu'ang Fang (presumably *blanfordi*). There is a possibility that the birds of Nan (and perhaps of Mu'ang Fang as well) are indeed *extensicauda* (from which, in my opinion, *exter* is inseparable); until, however, specimens in good winter dress are known from those areas, we have not the least evidence that they differ from the population of Chiengmai, which is certainly *blanfordi*.

## 3. *PRINIA INORNATA HERBERTI* Stuart Baker

*Prinia inornata herberti* STUART BAKER, Bull. Brit. Orn. Club, vol. 38, p. 39, 1918 (Bangkok, Siam).

*Range*.—East Siam and all Indochine, south of the territory occupied by *Pr. i. extensicauda*.

Riley<sup>5</sup> says: "In my opinion [*herberti*] is not a form of *inornata* at all, but of *Prinia blythi* of Java, which should not be in the same form group." He goes on to list differences between *blythi* and *inornata*, not one of which, from my point of view, is of more than subspecific value. Actually, the relationship of *blythi* and *herberti* to other members of the *inornata* group is much like that of *polychroa* and *cooki* to other members of the *polychroa* group (*vide infra*).

## IV

*Prinia flaviventris*, in one form or another, is now known to occur, however rarely, at suitable localities in all parts of Siam and Indochine. The greater part of the subregion is inhabited by a bird which has always been called *Prinia fl. flaviventris*, but which, while agreeing perfectly with that race in color, differs from it in its rather heavier bill and its acquisition in winter of a tail only slightly longer than that

<sup>4</sup> U. S. Nat. Mus. Bull. 172, p. 443, 1938.

<sup>5</sup> Idem, pp. 442-443.

of summer, thus approaching the very strong-billed *Pr. fl. rafflesi*, which shows no seasonal variation at all in length of tail. I propose to name this form

**PRINIA FLAVIVENTRIS DELACOURI, new subspecies**

*Type*.—Adult male, P.M.Z. No. 10301, collected at Chiengmai, 1,000 feet, North Siam, January 30, 1932, by H. G. Deignan.

The races now known from the Indo-Chinese countries, exclusive of Burma, are:

**1. PRINIA FLAVIVENTRIS SONITANS Swinhoe**

*Prinia sonitans* SWINHÖE, Ibis, 1860, p. 50 (Amoy).

*Range*.—In Indo-China: NE. Tongking.

**2. PRINIA FLAVIVENTRIS DELACOURI Deignan**

*Range*.—Pegu, Siam, and all Indochine, except those areas inhabited by *sonitans* and *rafflesi*.

**3. PRINIA FLAVIVENTRIS RAFFLESI Tweeddale**

*Prinia rafflesi* TWEEDDALE, Ibis, 1877, p. 311, pl. 6, fig. 1 (Lampongs, South Sumatra).

*Range*.—In Indo-China: Peninsular Siam, south of the Isthmus of Kra.

V

Since, as mentioned in my introduction, the southernmost race of *Suya crinigera auctorum* (type of the genus *Suya*) is clearly only subspecifically distinct from *Malurus polychrous* Temminck 1828 (Java), *polychroa* must take precedence over *crinigera* 1836 as the oldest name for the species.

The recognizable races of *Prinia polychroa* are seven or eight, depending on whether *Suya parumstriata* David and Oustalet (Fukhien) is distinct from the Formosan *Prinia striata* Swinhoe, which I have not seen.

**1. PRINIA POLYCHROA STRIATULA (Hume)**

*Blanfordius striatula* HUME, Stray Feathers, vol. 1, p. 195, 1872 [*nomen nudum*]; *ibid.*, vol. 2, p. 300, 1873 (Karachi).

**2. PRINIA POLYCHROA CRINIGERA (Hodgson)**

*Suya crinigera* HODGSON, Asiat. Res., vol. 19, p. 183, 1836 (Nepal).

### 3. *PRINIA POLYCHROA ASSAMICA* (Stuart Baker)

*Suya crinigera assamica* STUART BAKER, Bull. Brit. Orn. Club, vol. 44, p. 20, April 26, 1924 (Shillong, Assam).

*Suya crinigera assamica* STUART BAKER, Fauna Brit. India, Birds, 2d ed., vol. 2, p. 520, May 7, 1924 (no locality given).

### 4. *PRINIA POLYCHROA CATHARIA* Reichenow

*Prinia catharia* REICHENOW, Ornith. Monatsber., vol. 16, p. 13, 1908 ("Ta-tsieng-lu-ting in Szechuan").

*Range*.—Szechuan and NW. Yunnan.

Feathers of front, crown, nape, and mantle blackish brown, suffused with chestnut and margined brownish ashy to give a boldly streaked appearance (summer); equally boldly streaked, but the feathers overlaid with a rich dark rufous wash which masks the light margins and gives the bird a generally darker appearance (winter).

Two examples from Kiangyin, Kiangsu Province, agree perfectly with a series of *catharia* and not at all with a series of *parumstriata*. If these birds are not abnormal, it would seem that *catharia* follows the Yangtze from Szechuan to its mouth.

### 5. *PRINIA POLYCHROA PARUMSTRIATA* (David and Oustalet)

*Suya parumstriata* DAVID and OUSTALET, Oiseaux de la Chine, p. 259, 1877 (Fukhien).

*Range*.—East Yunnan, Kwangsi, Kwangtung, and Fukhien.

Olivaceous brown above, lightly washed with rufescent or ochraceous, the feathers of front, crown, nape, and mantle with faintly darker centers which scarcely appear as broad streaks (summer); much like *catharia* in winter but without the strong dark rufous wash and with the dark centers of the feathers much less clearly defined, especially on nape and mantle (winter).

Two specimens from Hunan Province are intermediate between *catharia* and *parumstriata*, having the obsolescent streaking of the latter race combined with the rufous suffusion of the former.

*Parumstriata* possesses considerable interest in that the summer dress shows its close relationship to the following more southern races, while the winter dress shows its equally close affinity with the preceding forms.

### 6. *PRINIA POLYCHROA STRIATA* Swinhoe

*Prinia striata* SWINHOE, Journ. North-China Branch Roy. Asiat. Soc., vol. 1, p. 227, 1859 (Hongsan, NW. Formosa).

7. *PRINIA POLYCHROA COOKI* (Harington)

*Suya crinigera cooki* HARINGTON, Bull. Brit. Orn. Club, vol. 31, p. 109, 1913 (Thayetmyo, Burma).

Upper parts dark olivaceous brown, almost free of rufescent or ochraceous wash, the feathers with faintly darker centers which scarcely appear as broad streaks (summer); similar, but with a faint rufescent wash and the obsolescent darker centers of the feathers a little more distinct, although less so than in the corresponding dress of *parumstriata* (winter).

It is remarkable that this species is known from the Indo-Chinese countries (exclusive of Burma) only in East Siam, Low Laos, Cambodia, and South Annam. It is still more remarkable that the isolated population inhabiting those districts should be identical with that of Thayetmyo but I have been unable to examine topotypical material of *cooki* and Dr. Delacour assures me that the two populations are indeed inseparable.

8. *PRINIA POLYCHROA POLYCHROA* (Temminck)

*Malurus polychrous* TEMMINCK, Nouv. Rec. Pl. Col. Ois., vol. 3, [livr. 78], pl. 466, fig. 3, 1828 (Java).

*Polychroa* closely resembles *cooki* of Annam at any season but differs in having the upper parts with an ashy, rather than a rufescent, wash. Worn specimens of the two races tend to approximate each other but the distinction here given is readily seen in fresh-plumaged examples.

The relationship between *Prinia polychroa* and *Pr. sylvatica* of India and Ceylon should be investigated by someone with better material than is available to me.

## VI

Chasen<sup>6</sup> has already, in my opinion correctly, made the Malaysian races of "*Suya*" *superciliaris* Anderson 1871 conspecific with "*Suya*" *atrogularis* Moore 1854, with the result that *atrogularis* becomes the proper name for the species. With the union of the genera *Suya* and *Prinia*, however, the Chinese subspecies becomes *Prinia atrogularis superciliaris* Anderson 1871 and the Bornean bird hitherto called *Prinia flaviventris superciliaris* Salvadori<sup>7</sup> is left without a valid name; for it I propose

<sup>6</sup> Handlist Malaysian Birds, p. 254, 1935.

<sup>7</sup> Ann. Mus. Civ. St. Nat. [Genova], ser. I, vol. 5, p. 249, 1874.

**PRINIA FLAVIVENTRIS CHASENI, new name**

Three well-defined forms of *Prinia atrogularis* occur within Indo-Chinese limits.

**1. PRINIA ATROGULARIS SUPERCILIARIS (Anderson)**

*Saya* [sic] *superciliaris* ANDERSON, Proc. Zool. Soc. London, 1871, pp. 212-213 (Momien [= Tengyueh], Yunnan).

*Range*.—Northern Burma, Yunnan, Kwangtung, Fukhien, Tongking.

**2. PRINIA ATROGULARIS ERYTHROPLEURA (Walden)**

*Suya erythropleura* WALDEN, in Blyth, Cat. Mamm. Birds Burma, Journ. Asiat. Soc. Bengal, vol. 43, pt. 2, extra No., p. 116, 1875 (Toungoo, Burma).

A series of five summer and eight winter birds from northern Siam and the adjacent parts of Laos differ from *superciliaris* in having the upper parts, throughout the year, more olivaceous brown, much less rufescent brown; the under parts, in winter, with less rufescence and that of a paler hue; the tail shorter than that of *superciliaris* at the same season and showing less seasonal variation in length than appears in the more northern race.

No toptype of *erythropleura* has been seen and the name is here applied to the Siamese population on the assumption that all birds of the same latitudes are likely, in this species, to be the same. If *erythropleura* be synonymous with *superciliaris*, the series before me is without an available name.

**3. PRINIA ATROGULARIS KLOSSI (Hachisuka)**

*Suya superciliaris klossi* HACHISUKA, Bull. Brit. Orn. Club, vol. 47, p. 53, 1926 (Dalat, South Annam).

*Range*.—Cochinchine, South Annam, Low Laos (Bolovens plateau).

In the Malaysian subregion appear also the two following forms:

**1. PRINIA ATROGULARIS WATERSTRADTI (Hartert)**

*Suya waterstradti* HARTERT, Nov. Zool., vol. 9, p. 568, 1902 (Gunong Tahan, Malay Peninsula).

**2. PRINIA ATROGULARIS ALBOGULARIS (Hume)**

*Suya albugularis* HUME, Stray Feathers, vol. 1, p. 459, 1873 (Acheen, Sumatra).

The type of *Burnesia dysancrita* Oberholser, which lies before me, shows that this name is a complete synonym of Hume's *albugularis*.











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(WITH 9 PLATES)

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# ARCHEOLOGICAL AND GEOLOGICAL INVESTIGATIONS IN THE SAN JON DISTRICT, EASTERN NEW MEXICO

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## INTRODUCTION

In continuance of a study of early horizons in North American archeology a Bureau of American Ethnology-Smithsonian Institution expedition spent the field season, June 20 to September 6, 1941, conducting investigations in eastern New Mexico. Members of the party, in addition to the writer, were: Dr. Kirk Bryan, Department of Geology and Geography, Harvard University; Herbert J. Dick, Jr., University of New Mexico; Robert Easterday, Colorado State Teachers' College; Walter B. Greenwood, Bureau of American Ethnology; S. Sheldon Judson, Harvard University; Bert E. Lohr and Edison P. Lohr, Loveland, Colo.; Donald D. McPhail, Michigan State College; Robert H. Merrill, engineer, Grand Rapids, Mich.; Robert M. White, Harvard University; Eugene C. Worman, Jr., Harvard University; Beulah J. Lohr, Linda B. Roberts, and Mrs. Merrill. Numerous interested scientists and amateurs from nearby southwestern and other institutions visited the camp during the progress of the work.

Most of the excavations centered around a site on the north rim of the Staked Plains  $10\frac{1}{2}$  miles (16.9 km.) south of the town of San Jon and 20 miles (32.2 km.) south of the Canadian River. At this location there is a shallow basin that appears to be a remnant of an old filled-in lake bed or series of ponds that had formed in the fill resulting when an original valley in the escarpment was blocked by sand deposits. The bottom of the basin is traversed by a series of deep ravines and broad arroyos (pl. 1, fig. 2) that come together and cut through the rim to join one of the intermittent tributaries of the Canadian heading in the brakes below. The local

name of the formation is Sand Canyon. Heavy erosion of the gully banks in recent years exposed deposits of alluvium and sporadic concentrations of animal bones including mammoth, bison, and deer as well as other smaller mammals, mainly of the Rodentia. Stone implements occurring near some of these outcroppings indicated that aboriginal hunters had been active in the area and suggested that both former camping places and associations between man-made objects and extinct species of animals could be found there.

The site was discovered by Keith Martin, a local ranchman, who reported the presence of the bones and showed the artifacts that he had found there to various people at the Museum of New Mexico and the Laboratory of Anthropology at Santa Fe, and at the University of New Mexico in Albuquerque. In the spring of 1940 Dr. Frank C. Hibben and a group of students from the Department of Anthropology at the University did some preliminary prospecting there and obtained a collection of animal bones and a few stone artifacts. In August of the same year the writer visited the site in company with Dr. Hibben. Because of the amount of work involved in a thorough investigation and the fact that its efforts were occupied with other archeological researches, the University of New Mexico offered to turn the site over to the Smithsonian Institution. The combination of features at the site and in the adjacent district was so promising that the offer was accepted. Permission to carry on the work was obtained from Mrs. George Wilburn, lessee, and Mrs. H. Bonem, owner, of Tucumcari, N. Mex.

Several factors were considered in making the decision to investigate the site. In addition to the occurrence of artifacts with fossil bones, there was the matter of the projectile points picked up from the weathered surfaces by Martin and found in situ by the University group. They are of the so-called Yuma type, a form purported to be of some antiquity but about which further data are needed to determine its true status. Furthermore, the location, some 130 miles (209.2 km.) south of the original Folsom bison quarry (Figgins, 1927; Roberts, 1935, 1940), and some 60 miles (96.6 km.) north of the important deposits along Blackwater Draw between Clovis and Portales where Folsom and Yuma materials occur (Howard, 1935; Roberts, 1940), as well as its proximity to some of the west Texas places where reputedly old finds have been made, seemed significant. In addition the area was the scene of considerable activity during late protohistoric and early historic times. It was hunting territory for numerous bands of the Apache—the Querechos of Coronado and



the Vaqueros of Benavides; possibly for some of the Jumanos—the Patarabueyes of Espejo and the Rayados of Oñate (Mera, 1935; Scholes and Mera, 1940); for occasional groups from the eastern Pueblos; perhaps for some of the Wichita roving that far west; for the later Comanche and Kiowa; and even some of the Pawnee. Coronado's party probably followed the Canadian north of the site and other Spanish explorers visited the region. One of the main Comanche trails, the northern, skirted the base of the bluffs. Numerous survey parties from the eastern States passed that way during and immediately after the Mexican War; the California emigrant trail from Fort Smith, Ark., followed the Canadian in 1849; and still later one of the famous trails of the cattle barons traversed the valley. All contribute a share of interest and enhance the possibility of adding to the fund of knowledge pertaining not only to the "early man" occupation of the region, but to later Indian groups and historic events as well.

The escarpment of the Staked Plains rising some 800 feet (243.8 m.) above the broad valley of the Canadian River is one of the striking topographic features of the district (pl. I, fig. 1). The brakes, from the rim to the plain below, are covered with juniper, piñon, and scrub oak, and there are sporadic clusters of cottonwood trees along the stream beds that start in the brakes and wind across the lower plain from the base of the bluffs. On top a sparse scattering of juniper and piñon extends back a short distance from the rim and occurs in protected places in gullies and ravines, but for the most part the upper level quickly merges into the vast, rolling, treeless terrain that so bewildered both the Spanish and early American explorers. Prior to the recent heavy cultivation of large areas for wheat and grain sorghums it was covered with a thick, heavy carpet of grass that furnished ample forage for the great herds of buffalo and antelope, as well as for the wild horses of the Canadian in historic times, that roamed its stretches. Several varieties of cacti, including the bushlike cholla or coyote candles, grow on the slopes of the escarpment and along the ravines, and yucca is fairly abundant. Wild grapes can be found in places along the base of the bluffs. There are several kinds of bushes with edible berries and numerous plants whose roots, tops, and seeds contributed in no small measure to Indian subsistence.

The winter and spring of 1941 were unusually wet in this district with an attendant abundance of plant forms. Among those noted were a number that are known to have been used by Indians in other

parts of New Mexico and it is quite possible that they may have served the peoples living here. Although it is not definitely known that all of the forms were present in earlier times, they are so widespread that it may be taken for granted that they were available. Included in this list are: The sunflower (*Helianthus annuus*) that furnished seeds for parching and for grinding into a paste used in thickening stews and making cakes; the four-o'clock (*Mirabilis multiflora*) the roots of which were used in tanning; purslane (*Portulaca oleracea*) that furnished greens; amole or yucca (*Yucca glauca*) with seed pods for food and roots for soap; datil (*Yucca baccata*) the fruit of which was eaten raw and cooked in various ways; rabbit-brush (*Chrysothamnus latissquameus*) the buds of which were eaten and the flowers of which were the base for a yellow dye; pigweed (*Amaranthus retroflexus*) that supplied fresh greens or was dried for winter use; lambsquarter (*Chenopodium leptophyllum*) the leaves of which were used as greens and the seeds of which were ground into meal; panic grass (*Panicum obtusum*) with seeds that were ground into a kind of flour; wild peas (*Lathyrus leucanthus*) that contributed the whole pod as well as seeds; wild potatoes (*Solanum fendleri* and *Solanum jamesii*) the small tubers of which were boiled with the skins on or were eaten raw with a white clay or talc to counteract certain unpleasant effects they otherwise might have.<sup>1</sup> Then, of course, there were the nuts from the piñons (*Pinus edulis*) and the prickly pears (*Opuntia* spp.) that were in high favor with the Indians.

The buffalo has disappeared, but a few antelope (*Antilocapra americana americana*) and white-tailed deer (*Odocoileus virginianus texanus*) can still be seen. Some of the local residents report that on occasions they have observed mule deer (*Odocoileus hemionus macrotis*) in the brakes. This is a little south and east of the normal range for that particular deer, but the animals would not need to stray far to wander into the district. Jack rabbits (*Lepus californicus melanotis*) and cottontail rabbits (*Sylvilagus audubonii neomexicanus*) are plentiful, the prairie dog (*Cynomys ludovicianus ludovicianus*) and pocket gopher (*Geomys breviceps llanensis*) are common. Coyotes (*Canis latrans*) were seen by members of the party, lynx or bobcat (*Lynx rufus baileyi*), badgers (*Taxidea taxus berlandieri*), a buff-gray fox (probably *Vulpes velox velox*, but this

<sup>1</sup> These plants were identified by Linda B. Roberts. For further information on native plants as sources of food in the Southwest see Castetter, 1935; Castetter and Opler, 1936.

identification is based on only fleeting glimpses of the animal), skunks (*Mephitis mesomelas varians*), rock squirrels (*Citellus variegatus grammurus*), striped and spotted ground squirrels (*Citellus tridecemlineatus arenicola* and *Citellus spilosoma major*), the hoary wood rat (*Neotoma micropus canescens*), and many kinds of small mice abound.

Birds are numerous in the locality and among those observed were: Lark bunting (*Calamospiza melanocorys*), the cowbird (*Molothrus ater ater*), mourning doves (*Zenaidura macroura marginella*), western meadowlark (*Sturnella neglecta*), horned lark (*Otocoris alpestris leucolaema*), western mockingbird (*Mimus polyglottos leucopterus*), kingbird (*Tyrannus tyrannus*), cactus woodpecker (*Dryobates scalaris cactophilus*), piñon jay (*Cyanocephalus cyanocephalus*), cliff swallow (*Petrochelidon albifrons albifrons*), western lark sparrow (*Chondestes grammacus strigatus*), Arizona scaled quail (*Callipepla squamata pallida*), road runner (*Geococcyx californianus*), western burrowing owl (*Speotyto cunicularia hypogaea*), sparrow hawk (*Falco sparverius sparverius*), western redtail hawk (*Buteo jamaicensis calurus*), nighthawks (*Chordeiles minor henryi* and *Chordeiles minor howelli*), Bullock's oriole (*Icterus bullocki bullocki*), and the Cassin sparrow (*Peucaea cassini*). Wild turkeys formerly were abundant along the Canadian near the Texas border but have not been reported since the middle of the nineteenth century. They probably were the eastern form (*silvestris*) and had worked their way up the river and into eastern New Mexico.

There are several kinds of snakes, including the diamondback and prairie rattlers, as well as a few lizards and the horned toad. From the standpoint of the flora and fauna the district by and large is still one that would hold considerable attraction for aboriginal peoples.

The general problem was attacked from several angles. One pertained to the locating of archeological materials and discovering what the associations were, if any, between different types of artifacts and animal remains. In this connection there also was the matter of determining to what extent the various kinds of stone tools and the bones could be correlated with the several strata in the fill. Then there was the question of a sequence in implement types and the possibility of obtaining important information on the relationship between the Yuma and points from already established cultural horizons. Another phase consisted of a careful study of the material in the fill in the basin at the main site, of deposits in the general

area, and of possible correlations of both with geologic phenomena of known age. To facilitate the recording of archeological information and to aid in the geologic studies a detailed 5-foot (1.524 m.) contour map of the basin and its gullies was prepared by Mr. Merrill.

Results were more gratifying in some cases than in others. This is in part attributable to an insufficient quantity of archeological evidence rather than to its quality, and to the fact that certain phases require further work. On the whole, however, an interesting outline of developments in the area is apparent from present information.

### ARCHEOLOGICAL WORK

The archeological activities, under the writer's direction, were carried on by the students in the group. The grid system was followed in the digging. Areas to be investigated were staked off in 5-foot (1.524 m.) squares, the lines running east-west and north-south, and exploratory trenches were laid out in 5-foot widths with their lengths continuing as required on the basis of 5-foot units to provide consistency in the records and in order that the sections would be uniform in case it was found necessary to expand the trenches into larger areas. The men were given separate sections, each working his own from the surface to the bottom of the excavation (pl. 2, fig. 1). The material was removed layer by layer, following the natural strata, and the vertical and horizontal positions and the nature of the earth surrounding all objects found were carefully recorded. On the completion of a section a scale drawing was made of the face of the next section before work was started on it. In this way profiles showing the nature of the deposits as they occurred at 5-foot intervals throughout the digging were made available for study and as a part of the data pertaining to the excavations. The archeological material presented no handling difficulties, but in the case of the animal bones it was often necessary to harden them with preservatives and to apply plaster jackets before removal.

Excavations in three sizeable areas and four trenches in and around the basin (fig. 1), digging in four places on the level top of a terrace in the brakes, midway between the rim and the plain below, and in buried hearth levels exposed by gullies in the lower plain, produced an interesting series of implement types with geologic evidence for a sequence in some of the forms. This was also true for some of the animal bones, although the number of variations involved was not as great. Four types of projectile points came from the basin and its environs and from the terrace site. They occurred in four



stratigraphic horizons and while actual superposition of specimens was lacking, the geologic nature of the layers is such that there seems little reason to doubt that the sequence indicated is correct. A fifth type was found in a buried occupation level in the lower plain. Its position in the sequence is somewhat doubtful at present writing, yet it seems to be approximately contemporaneous with the third or next to most recent in the series from the basin.



FIG. 1.—Map showing outline of main arroyos in the basin and the break through the escarpment. Location of work areas, trenches, and places where bones were found without accompanying artifacts are also indicated.

The earliest type of point, a rather roughly chipped, thick-bodied blade with a square base, parallel sides and rounding tip (fig. 2, *a*), occurred in a layer of dark earth corresponding to the top level of the silt in one of the old ponds or lake beds. The point in general might be considered as an example of the Indeterminate Yuma (Wormington, 1939), but the lack of many of the characteristic minor details makes its assignment to that classification debatable. This doubtful status is accentuated by the fact that many obviously unrelated forms have been lumped together under the name Indeter-



minate, and it is very much a question whether any of them should be considered as belonging in the Yuma category. The uncertain nature of the class was emphasized by the discussions at a conference held at the Laboratory of Anthropology in Santa Fe, N. Mex., in September 1941 (L. L. Ray, 1942; C. T. Hurst (The Editor), 1942), when it was proposed that the Indeterminate group be dropped from the Yuma series. Consensus was that as each of the forms became established it could be named on the basis of its place of origin and proper relationships. In view of this it probably is best, for the time being, to refer to the present type as the San Jon point, adding the proper qualifier when its affinities have been determined.

The San Jon point was associated with the remains of a large bison, probably the extinct *taylori*.<sup>2</sup> The bones from this level are completely fossilized, and in many cases articulated members were so firmly mineralized that they were lifted from the earth as a unit. Numerous examples of articulated feet and lower leg bones were found in upright positions in the upper part of the silt or alluvium (pl. 3, fig. 1). They definitely suggested an animal wading out to drink, becoming inextricably mired in ooze and perishing there. Perhaps the Indians, certainly some of the carnivores in the area, preyed on the creatures trapped in this fashion because in many cases bones from the upper parts of the legs and the body were either entirely missing or else were considerably scattered.

The geologic age of this deposit is still to be established. At another part of the site, however, a portion of a true Folsom point was found weathering out of the same layer in association with fragments of similarly fossilized bone. This, coupled with the fact that a large bison is involved, points toward possible contemporaneity with the Folsom horizon, one of the oldest thus far recognized in North America and dated in the closing stage of the Pleistocene (Antevs, 1935; Bryan and Ray, 1940). But because the Folsom specimen was not wholly in situ and represents only a single occurrence it can be regarded merely as an indication. On the other hand the presence of man-made objects with extinct bison remains and the occurrence of mammoth bones, teeth, and tusk fragments in the same stratum a few feet away, although no direct associations have thus far been

<sup>2</sup> This material was identified by Dr. C. Lewis Gazin, assistant curator, division of vertebrate paleontology, U. S. National Museum, who stated that it obviously was from an extinct form closely approximating *taylori* in size, but because only lower jaws and leg bones are available for study the species cannot be indicated with certainty.

found between the latter animal and artifacts at this location, implies some antiquity. That contemporaneity of Indians and the mammoth in this region was within the bounds of possibility is indicated by the finds near Clovis (Howard, 1935; Cotter, 1937), at Sandia Cave (Hibben, 1941), and in various Texas sites (Sellards, 1940).

The second type of point, a characteristic Yuma of the form designated the Collateral (Wormington, 1939) and since the 1941 Santa Fe

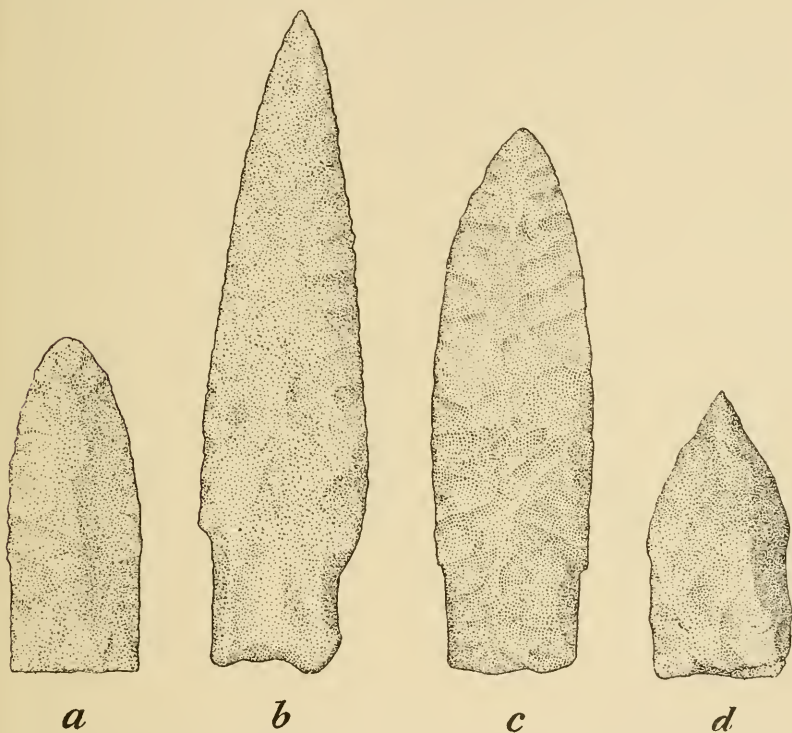


FIG. 2.—Some projectile point types. a, San Jon; c, Collateral or Eden Valley Yuma; b, and d, unnamed forms. (Actual size.)

conference tentatively called the Eden Valley Yuma, comes from a mixed layer of reddish clay and sand and is found in association with bones from an essentially modern species of bison, a much smaller animal than that of the lower level. The bones show some fossilization, although it is in much less degree than that of the first group. Geologic evidence is that this horizon was separated from the first by an appreciable period of erosion followed by marked deposition. This argues for considerable time lapse and a much younger age for the cultural material. The Collateral or Eden Valley

Yuma at San Jon has an elongated subtriangular shape with slightly convex edges, a rudimentary tang formed by a slight inset on the edges near the base, and a slightly convex base (fig. 2, *c*). There is a suggestion of the median ridge on the faces and the inset edges near the base are smoothed. All the Yuma points reported from the site have not been seen by the writer as some of the earlier finds have been scattered, but those that were studied conform to the above description. It is possible that some of the Oblique Yuma (Wormington, 1939) may be there, although the presence of one form does not necessarily imply that the other also will be found. There are numerous cases where only one of the types occurs at a site.

The third type of point, one with a long, leaf-shaped blade, rounding shoulders, and a roughly straight tang with a slight bevel to the left, and a concave base (fig. 2, *b*), is found at a little higher level in deposits essentially the same as in the case of the preceding form. This point suggests some of Ray's Clear Fork types (C. N. Ray, 1938), belongs in the same category as one from the Taos Plateau reported by Bryan and Butler (1940), possibly has some relationship to Sayles' Brazos River forms (Sayles, 1935), and also bears some similarity to points from the Big Bend region identified as forms frequently found in Pecos River sites<sup>3</sup> (Kelley, Campbell, and Lehmer, 1940, pl. 5, fig. 1, *b*, upper left; fig. 2, *b*, left); yet it is sufficiently different to make correlation with the latter questionable. The only animal remains associated with these points are those of modern bison, the bones showing no traces of fossilization. The chief distinction between the remains of this and the Yuma horizon appears to be in the fossilization of the bones. In general the degree or absence of mineralization has little value as a criterion because of the varying rates at which it takes place under diverse conditions and in different localities. When the material comes from a small area at a single site where there is no difference in conditions, however, it probably does have some significance and can be considered as giving at least an indication of relative age. Hence on the basis of the nature of the bones and of the earth from which they and the points were dug it seems evident that they are somewhat, although not markedly, later than the Yuma.

The fourth type in the series is actually a group of several subtypes of the small, notched and tanged arrowheads common at recent Indian sites. Sporadic examples are found on the surface around the basin, on the slopes of the brakes, and on the plain below. In the excava-

<sup>3</sup> Not the type of point named the Pecos River point, however.

tions, however, they occur just below the present sod line or, as in the case of those from the terrace in the brakes where there is no grass, are from 2 inches (5.1 cm.) to 4 inches (10.2 cm.) beneath the surface in the upper part of an ash- and charcoal-stained deposit underlying a layer of sterile sand. Curiously enough none of these seems to belong to any of the types identified as characteristic of the Apache, Wichita, Jumano, or Panhandle groups (Sayles, 1935) that might be expected to have left a few points in the region.

The triangular form with broad, expanding tang with convex base (pl. 4, *a*) appears sporadically over most of the southern plains, is occasionally seen in collections from the northern plains, occurs in some eastern Pueblo ruins, and may be found in sites east of the Mississippi River. It apparently does not occur in large numbers in any one locality and has not been correlated with any particular horizon or specific cultural group, but it undoubtedly is a relatively late type.

The same is true for the group with a longer, expanding tang and more rounding base (pl. 4, *c*). A comparable point is reported from a rock shelter in the southern escarpment of the Staked Plains in Winkler County, Tex., some 220 miles (354.1 km.) southeast from the San Jon site (Holden, 1938, pl. 28, No. 10). There the association included potsherds, some of Pueblo origin, other types of projectile points, knives, scrapers, drills, bone and shell artifacts. The culture represented is considered to be non-Puebloan, many of the points and artifacts seem to be Sayles' Wichita and Jumano types although other groups are also included, and evidently does not belong in an early category.

The triangular point with slightly convex and serrated edges, medium tang and concave base (pl. 4, *b*) suggests some of the Texas forms from the Edwards Plateau section, might possibly be derived from some of the bifurcated-base types found there, and also has a resemblance to examples occurring sporadically in the eastern periphery of the Pueblo area, yet it does not appear to have definite affinities with established cultural phases. Perhaps, like the others, it represents a minor type that had a rather widespread distribution and as far as present knowledge goes is without any particular significance.

The last in the group (pl. 4, *d*) is a type in which the basal portion constitutes a much larger proportion of the blade than is usually the case. The tip end is triangular in shape, while the section below the side notches is roughly rectangular with a deeply concave base.



Slightly variant examples of the type have been reported from numerous sites, mainly of the Classic and later periods, in the Pueblo area where they generally are considered as "unusual" forms (Cosgrove, 1932, pl. 51, *a*; Kidder, 1932, fig. 6). They probably bear some relationship to the more highly developed points found in Oklahoma, some of the southern States, and even in parts of Mexico, that are characterized by such deep basal concavities that they appear to have wings. Beyond their late horizon, however, they do not seem to have any special local significance and certainly cannot be regarded as a criterion for the presence of any specific group in the area. All four of these types of points are in association with bones from modern bison, deer or antelope, and jack rabbits.

The fifth type, found in a buried occupation level in the lower plain (pl. 3, fig. 2), is a rather stubby form with roughly parallel sides, flat base, and sharply tapering tip (fig. 2, *d*). First thought was that the implement was a drill made from a broken point, but careful reconsideration and study of several examples indicates that it probably was a form of projectile. In a general way it bears resemblance to some of the points from the Edwards Plateau district in Texas and also some of those from the Big Bend region, yet it is sufficiently distinct to be considered as representing a separate class. Possible relationships may be determined by future work in the region. Associations in this case consisted of modern bison, deer, and bones from small mammals. The type, as previously mentioned, appears to be contemporaneous with the third main group, yet eventually may prove to be somewhat older.

Projectile points were the only artifacts obtained from the oldest and subsequent Yuma horizons, unless a few nondescript flakes capable of utilization as knives or scrapers be considered as tools, and there is no information regarding other kinds of implements comprising the complexes to which they belonged. Further data along this line are essential to a proper understanding of the subject as a whole. Several kinds of scrapers, knives, choppers, hand hammers, and grinding stones were associated with the later type points. In the case of the fourth series there was the addition of potsherds.

The ubiquitous snub-nosed or end scraper (pl. 4, *c-k*) is one of the more prevalent forms in the group of scrapers. As is usually the case, most of the examples are of the uniface, planoconvex type with the flat side showing little or no chipping and the curved side having had just enough flakes removed to give the implement its characteristic shape. The convex, broad end and two edges were retouched by the



pressure method, the fine flaking producing sharp scraping surfaces. The smaller end, which on most examples still shows the bulb of percussion produced when the flake was struck from the original nodule, rarely has any flaking. An exceptional specimen is shown in plate 4, *k*, where the smaller end was given a concave edge of the form that was used for scraping and smoothing arrow shafts. No examples were found with a small, sharp point for perforating or graving purposes. In some localities these are a fairly common feature on snub-nosed scrapers and may occur at various places on the implement. In some cases they are at one of the corners formed by the convex end and one edge, occasionally they may be noted at both corners, or they may be along one of the edges or at the small end. Whether the absence of the feature from the San Jon examples is purely coincidence in that specimens bearing it just weren't found or is a matter of significance is not known at present. Taken as a group or singly, there is nothing to distinguish the scrapers in this series from similar forms found elsewhere in either Plains or Pueblo sites and they cannot be considered as a criterion for cultural or period identification. They apparently were concomitant with hunting among most Indian groups.

Side scrapers of simple form were common (pls. 5, 6). They were made from flakes of various sizes and shapes and in most cases exhibit a minimum of flaking, except along the functioning edge which was given a low-angled bevel. A few specimens have a fine, secondary flaking or retouch along the working edge, but for the most part the regular flaking seems to have been sufficient and there are examples where it occurs on only a portion of the edge. As a matter of fact numerous sharp flakes undoubtedly were used as scrapers without any attempt being made to better the edges through the flaking process.<sup>4</sup> This is particularly true of various quartzite forms occurring in abundance at the places where the other types were found. Such flakes break away from a core or nucleus with a fine, straight edge that will stand considerable abuse before being dulled to the extent that it is no longer efficient. While such implements are in use, small flakes are generally knocked off the edge. This is a good criterion for identifying utilized flakes. Numerous examples in the collection show this feature. A large majority of the working edges are convex, only a few are straight, concave forms are rare, and there is no example of a double-edged tool in this series.

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<sup>4</sup> Flakes found in association with the San Jon and Yuma points belong in this category.

Closely associated with the foregoing implements is a similar group that is arbitrarily considered to consist of rough flake knives. The main distinction is that of thickness and the nature of the functioning edge. In the case of the knives the flakes are much thinner and the edge has an acute, longer-tapering bevel. Both scrapers and knives of this type are commonly regarded as fortuitous flakes and little attention is paid to them. They seem to have been an important part of the implement complex in this district, however. The closest similarities between them and artifacts from other localities are found in a series from caves along the Cimarron Valley in northeastern New Mexico and western Oklahoma (Renaud, 1930). The latter were part of a complex that has been considered as a primitive form of Basket Maker culture and although, because of peripheral lag, it may be later chronologically than the material from the main Basket Maker centers farther west, it is, if correctly identified, older than the San Jon specimens. In view of this situation, perhaps the main significance in the similarity of forms is their indication that in this general region the hunting peoples over a long period of time tended to rely on implements produced with a minimum of clipping.

Better knives of the more conventional type consist of bifaced blades of a general broad-leaf shape with rather blunt points and broad, convex base (pl. 6, *h, i*). The workmanship on these implements is not so good as that on the projectile points, but they are definitely made tools. There is nothing, however, to distinguish them from similar artifacts scattered abundantly and widely over most of the Plains area. Fragments from a diamond-shaped, double-ended or four-edged, beveled type of knife that is common in districts farther east in Texas and Oklahoma (Poteet, 1938), and extending northward along the western edge of the Plains, were found, but no complete specimen was obtained. This type of knife has been attributed to the Wichita (Sayles, 1935), yet it has been found under conditions suggesting that it may derive from other, and in some cases possibly older, groups. Whether the form actually was made in the San Jon district or was an importation is an unsettled problem. On the basis of its small representation and the lack of complete specimens it would seem to belong in the trade category. Sayles, however, notes that it was a common Panhandle artifact and the present fragments appear to be of Poteet's type B which is believed to center in the Panhandle. Hence it may be at home in the San Jon collection. The kinds of stone used in this instance are not much help as they occur locally as well as farther east. The implement

unquestionably belongs to the general bison-hunting complex of the Plains and where found in Pueblo sites of the eastern periphery is an introduced form and good evidence for trade relations. (Kidder, 1932, pp. 30-34).

Choppers consist of large pebbles or fragments of stone with broad flaking along one side or an end (pl. 7). In rare cases there was a little secondary chipping but they mainly were fashioned, like many of the scrapers, with a minimum of effort. Frequently the removal of one or two flakes sufficed to form a satisfactory working edge. The remaining smooth surfaces would serve to protect the hand of the user. From their occurrence in the excavations it was evident that these objects had been employed in cracking and splitting bones. This type of tool is commonly found at sites attributable to hunting peoples or those who depended on game for a large part of their sustenance.

Hand hammers are simple round or ovoid-shaped pebbles that generally exhibit a slight amount of pecking or pitting, probably the fortuitous result of use, along one side or on each end (pl. 7). They are of a size that can be gripped in the hand, 3 inches (7.6 cm.) to 5 inches (12.7 cm.) in diameter, and no doubt served for knocking flakes from nodules in the manufacture of implements and for general pounding purposes under conditions where such a tool was needed. Some are suggestive of what has been termed the Plains Maul (Sayles, 1935), although in no case is there any indication of polish around the central portion of the body nor the slightest trace of an encircling groove, features common to that implement. The Plains Maul usually is associated with the complex of agricultural and seed-gathering peoples. One of its purposes may have been that of pecking out depressions in stones intended for grinding and in shaping the smaller stones used with them, in which case it would be most efficient as a hand tool. That it had other functions, however, is indicated by the polished central portion or shallow groove evincing hafting in some sort of handle. There was not much indication that the inhabitants had practiced agriculture in the vicinity of the San Jon site, but that they took advantage of the abundance of natural products is suggested by the presence of hand stones or manos and milling stones or metates. Both of which may have been shaped by artisans employing hand hammers or mauls of the type found here.

The hand stone or manos for grinding are rather nondescript and all are of the single hand size (fig. 3). Some are oval in outline with one flat and one convex grinding face. Others are roughly

circular with one flat and one convex face. Still others are circular with two flat faces and a wedge-shaped cross section. There are examples that are little more than natural pebbles with a single flat or only slightly convex face. In some cases the edge between the two grinding surfaces was pecked, in others it was not. There

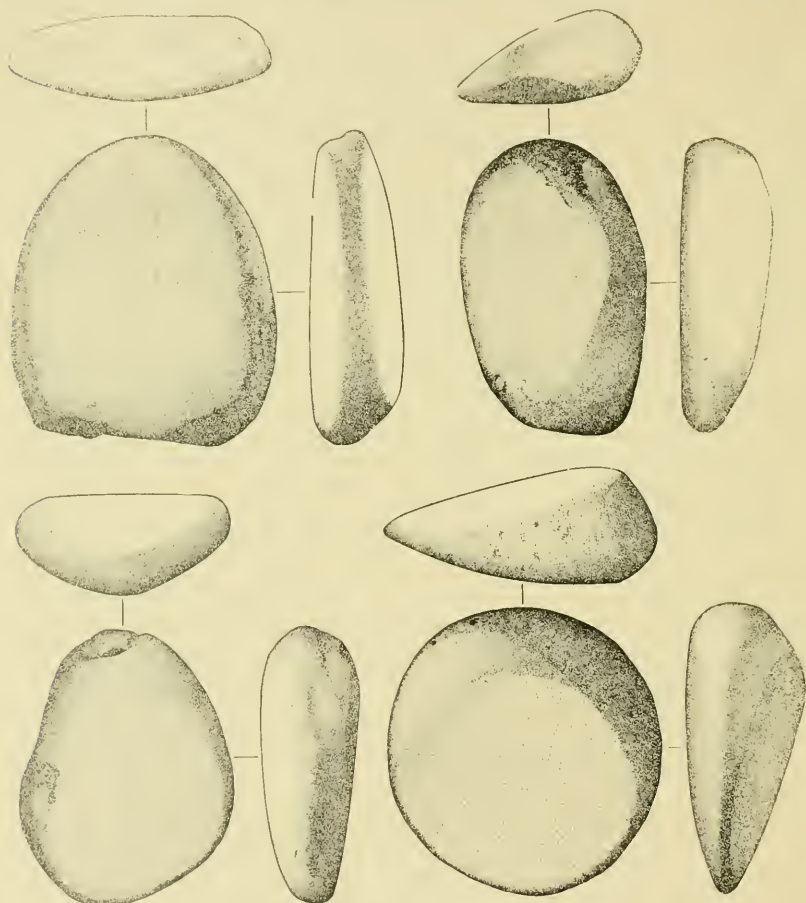


FIG. 3.—Manos or hand grinding stones. (One-third actual size.)

apparently is no correlation between outline, grinding surface forms, and the pecking of the edges. The latter may or may not be present on any of the two-faced forms. No one type of mano seems to have prevailed over the others or to be characteristically associated with one type of point. In general they are similar to those found at most sites throughout the region occupied by users of native food plants. In contrast to many locations, none of the San Jon examples has a



pit or depression in the face. The latter implements possibly were a combination type that could be used either as a grinding stone or as a hammer, the pits or depressions making it easy to hold the stone between the thumb and fingers and strike with the edge. Hard nuts and seeds could be cracked in this fashion and then be ground by rubbing with the flat surfaces without the necessity of changing tools in the process.

The metates or nether milling stones are of two types. One is a thin slab of stone with a shallow, oval or circular bowl and the other is a deep, narrow, troughlike stone that actually might be considered as boat-shaped. Little effort seems to have been made to give form or shape to the thin examples. A roughly rectangular or polygonal slab was obtained, and a shallow basin was pecked in one face. Through use the basin would be enlarged and deepened. The trough or boat-shaped type, fashioned from large tabular blocks, was given some external dressing, the rounding of sharp edges and the removal of projecting points, but most of the work was on the interior and pertained to the pecking of the groove or trough. The latter extended a greater part of the length and width of the block. The deepest portion was along the center with the bottom curving up toward the ends, the sides being fairly vertical. The ends of the trough were closed, not pecked open as in the case of the Pueblo milling stones. Both of these metate forms are reported for the Jumano and Panhandle groups, while the first is also attributed to the Wichita (Sayles, 1935) and extends northward into other portions of the Plains area. The difference in metates no doubt accounts for the difference in manos. The circular forms would be used for the most part with the shallow bowl type, the grinding being done with a circular motion of the hand and arm, while the longer oval examples would serve in the trough form, the grinding being accomplished with a backward and forward movement of the hand stone.

Materials used in the manufacture of implements consisted of chalcedony, chert, jasper, quartzite, dolomite, sandstone, and granite. The projectile points of the San Jon and Yuma types were made from gray and mottled chert. The points in the third group are all of quartzite, gray, brown, red, or yellowish white. There is greater variety in the fourth group, chalcedony, jasper, chert, and quartzite. Fifth type points were made from gray or white quartzite. The fragment of Folsom point is of dolomite. The snub-nosed scrapers are of jasper, chert, dolomite, and quartzite. Other types of scrapers are mainly quartzite, with a few of jasper. The flake knives are



mostly quartzite, although there are sporadic examples of jasper and chert. Jasper and dolomite were used in the four-edged knives. Choppers were made of quartzite and from granite pebbles. Hand hammers are quartzite, granite, and sandstone. Manos and metates are sandstone. Most of these materials could be obtained locally and there are several places on the slopes of the brakes where nodules have weathered out from the formation. At each of these locations there is definite evidence of workshop activities in the form of numerous chips and flakes, fragments from partially completed implements and hammer stones used in the breaking of nodules. Identical scraps and flakes were found in the digging around the basin and on the terrace site, showing that some of the material was carried back to camp and worked on there. Some of the chert probably came from deposits farther east and was mostly imported in the form of completed implements as there is little of that kind of stone in the chipper's debris around the basin. The dolomite is the silicified form generally known as Amarillo dolomite which occurs along the Canadian River and some of its tributaries and which was obtained by the Indians from extensive quarries near Amarillo, Tex. Some of this material undoubtedly was taken to San Jon, possibly in the form of blanks to be fashioned into completed tools at the maker's leisure, as small bits and flakes of it are found in the chips from the occupation areas. Sandstone and granite pebbles are available at numerous places in the vicinity of the basin and other sites.

One kind of stone used in snub-nosed and other types of scrapers seems to be a silicified sandstone that has actually become a quartzite. It has a characteristically laminated appearance suggestive of shale (pl. 5, center right), but in contrast to that material is very hard and compact. It is of particular interest because flakes, nodules, and implements made from it are abundant at a site lying between Big and Little Tucumcari Mountains a few miles south of the town of Tucumcari. Present evidence is that it was not extensively used elsewhere in the region which suggests a possible relationship between the occupants of the basin area at San Jon and the site near Tucumcari. This is also indicated by other factors and if contemporaneity should be established it would be of significance in the matter of certain geologic correlations still to be demonstrated. The source of this material has not been definitely located as yet, but it unquestionably is in the immediate district.

The potsherds found in association with the artifacts and fourth type points occur only in small fragments and are not numerous.

While they indicate that the people had a knowledge of and possessed some pottery, they also suggest that it was not a highly important trait in the complex as far as activities around the basin were concerned. Most of the sherds are from a buff or brownish-colored ware with smooth surface and hard, compact paste. The tempering material, as studied with a hand glass, appears to be sand. In a few cases there is a slight admixture of mica. None of the fragments show any form of decoration. Both bowls and jars seem to be represented. As a group the sherds fit the description for Sayles' Panhandle wares, although no paddle-marked examples were found. The Panhandle wares are associated with house ruins concentrated along the Canadian River (Sayles, 1935, p. 84) and on the basis of associated sherds from the Rio Grande have been dated as about middle fourteenth century. The affinities of the wares have not been definitely established. They probably belong to the broad basic form represented in the pottery of the Wichita and the Jumano which in turn points toward the Caddo. It is possible that the presence of such sherds near the basin at San Jon is to be attributed to hunting parties from the Canadian settlements to the northeast and that the small number is due to the fact that people on the move rarely burdened themselves with many pottery vessels.

There are a few black-on-white sherds from vessels that probably belonged to a type of pottery from an adjacent area to the west. This form has been called Chupadero Black on White (Mera, 1931) and is one that is commonly found in association with brown wares such as those represented by the sherds in the present collection. Chupadero Black on White is a Pueblo ware that was taken over bodily and adopted by the makers of the brown wares (Scholes and Mera, 1940, p. 293). Traces of it have been found as far east as the sand-dune camp sites in western Texas (Mera, 1935, p. 30). It was a late development out of an earlier type of Pueblo ware and seems to have been absorbed into the ceramic complex of the brown-ware region during the thirteenth century. It apparently persisted into early historic times and its presence in an assemblage of materials dating from the late fourteenth or early fifteenth century in the San Jon district is wholly in keeping with the general picture. Although both bowls and jars were made in this ware, jar fragments only were found during the San Jon investigations.

The occurrence of actual hearths was noted only in the horizons represented by the fourth and fifth point types. However, scattered pieces of charcoal and sporadic ashes were found in all of the archeo-

logical levels. In no case was the hearth an actual fire pit lined with stones or stone slabs. They were simple basins in former surfaces of occupation, were roughly circular or oval in outline, and were comparatively shallow. They ranged from diameters of 1 foot 4 inches (40.6 cm.) and 1 foot 6 inches (45.7 cm.) to 2 feet (61.0 cm.) and 3 feet (91.4 cm.), and from depths of 5 inches (12.7 cm.) to 8 inches (20.3 cm.). All of those examined contained ashes, charcoal, pieces of fire-burned rock, and sporadic chips and spalls from implement making. In a few cases charred fragments and splinters of bone, even complete small bones, were found mixed with the other debris. No traces of a habitation, tent circle, or shelter occurred in the vicinity of any of these hearths. As a matter of fact no such indications were found in any of the excavations. The probabilities are that any dwellings used by these people were of a temporary nature, tents made from buffalo skins being the most likely form, and as a consequence little evidence remains of their former placement.

#### GEOLOGICAL STUDIES <sup>5</sup>

Considerable progress was made in the study of the deposits and their possible age. This phase of the investigations was carried on by Dr. Bryan and Mr. Judson. Two lines of approach were followed. The first pertained to the belt of plains between the Staked Plains escarpment and the Canadian River, and the second to the archeological site at the basin. In the plain three stages of alluviation followed by periods of erosion, arroyo cutting, and the formation of sand dunes were established. This sequence has many similarities to deposits in the Hopi country in Arizona (Hack, 1942) and the Big Bend region in Texas (Albritton and Bryan, 1939) but because of insufficient field work is subject to revision.

Interesting items appear in the sequence, even though the results are regarded as still tentative. The last cycle of erosion, continuing at the present time, is characterized by arroyos and sand dunes. The beginning and heavy cutting of the arroyos representing this stage appears to belong to the decade from about 1900 to 1910. The formation of the first dunes in the present series started about 1910. The

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<sup>5</sup> The present summary is mainly for the purpose of rounding out the account of the expedition's activities and to indicate the archeological concomitants of the results. It is based on notes furnished by Bryan and Judson and on statements made during discussions of the problems in the field camp. The authoritative and detailed geologic report will be issued by Bryan and Judson when their studies are completed.

third alluviation is indicated by loose and friable alluvium. Fire pits, animal bones, and stone artifacts, late in type, occur in this layer. The preceding stage of arroyo cutting and wind-blown sand, the second erosion interval, is correlated with Pueblo type potsherds that date in the period 1300 to 1540. The second alluviation is characterized by an alluvium, humic in places, with irregular, hollow, twig-like limestone concretions (calcareous tubules) in the finer portions. Fire pits, artifacts, and bones from modern bison are found in this level. The first erosion period was marked by arroyos and sand-dune formation, but thus far is not correlated with any evidence of human activity or animal remains. The deposit of the first alluviation contains large limestone concretions and compact humic alluvium in small bodies. Mammoth, sloth, and horse bones have been found in this horizon. Projectile points purportedly of Folsom and Yuma types are supposed to have come from this layer, but the authenticity of this occurrence and the kind of Yuma involved remains to be established. If substantiated, however, and the Yuma proved to be of the Indeterminate type the combination of features would be an important link in correlating the plain deposits and those in the basin on top.

The deposits in the basin form a complex but definite sequence, one that is in part reproduced in the next gulch to the east. There are 11 stages in all and, as previously suggested, the sequence is related to the filling of an original valley in the escarpment with layers of sand, the "basal sand" of the section. The last or present stage is characterized by the deep ravines and the broad arroyos in the basin and the continuing erosion of today. Preceding this was an interval of alluviation characterized by coarse alluvium that remains as terraces. The small barbed arrowheads, potsherds, and grinding stones probably belong to this horizon. The disconformity between this layer and the next lower alluvium is marked by deep, narrow arroyos. The latter were cut into alluvial fill consisting of reddish clay and sand. It is in this horizon that the Yuma (Collateral or Eden Valley) and third type points belong. Broad, shallow arroyos characterize the disconformity between this layer and the underlying alluvium composed of a sequence of clay, red sandier alluvium, and clay. The San Jon point and extinct bison and mammoth come from this deposit, the lowest level for either animal or human evidence. Below this is a layer of water-laid ash, volcanic in origin, resting on an iron cap and associated clays resulting from the deposition of limonite and clays under wet conditions. The iron



cap and clays were laid down in the hollows in the top of the white and buff cross-bedded sand filling the basinlike valley that had been formed in the top of the Tertiary beds underlying the area.

The question of the relationship and the correlation between the two sequences is an important one. Although there are certain indications that are suggestively significant, more work is needed to establish them as facts. On the basis of the similar circumstance of the alluvium of the first alluviation in the plain sequence being subsequent to a deposition of volcanic ash and the lowest alluvium of the basin sequence resting on such material, that both contain similar faunal remains, and that Folsom and possible Yuma points are reported from them, it would seem that they are approximately the same age. Because of the uncertain archeological evidence for the presence of Folsom and Yuma material in the first alluviation and of Folsom at the basin site such a tie can be regarded only as highly tentative at best. There is an additional complication in the nature of the Yuma points involved. If those from the first alluviation are the Indeterminate, even perhaps the San Jon type, the case is much stronger than it would be if they are the Collateral or Eden Valley form, as the latter definitely occurs in a much later horizon at the basin. No doubt much of the difficulty will disappear when there is more complete geologic and archeologic information from which to draw conclusions. At present it is not possible to estimate how long a period of time is represented by the first arroyo-cutting cycle and the second period of alluviation; hence it cannot be indicated how many years before the 1300-1540 second arroyo stage the first alluviation ended.

While studying the deposits in the valley floor some miles west of the main site Mr. Judson found an interesting cache of 44 stone implements. The artifacts, consisting of five large blades (pl. 8), end scrapers, side scrapers, and flake knives (pl. 9), had been placed in a hole beside a fire pit. The blades were lying side by side in a line extending in a general east-west direction. The other specimens were grouped around and above the blades in no particular order. The fire and cache pits were exposed by the caving of a gully bank. Their tops were 2 feet (61.0 cm.) below the present surface. The overlying deposits consisted of a layer of structureless sand containing numerous charcoal flecks, a layer of red-clayey sand, and the layer of modern buff-white blow sand. The pits were dug into a layer of water-laid buff-colored sand to a maximum depth of 8 inches (20.3 cm.). This layer corresponds to the third alluviation period



in the sequence for the valley plain. On the basis of the evidence from Pueblo type potsherds, previously mentioned, Judson concluded that the earliest possible date for the third alluviation was in the late 1400's. Hence at most the specimens could only just antedate the early historic period, and it is more likely that they actually belong in that stage.

Neither in the type of the implements nor in the material from which they were made, a gray chert, is there any suggestion of relationship to the artifacts excavated in and around the basin at the main site. The absence of projectile points adds to the difficulty of attempting to correlate the material with any definite group or cultural horizon. The writer has seen blades and scrapers of this type, made from similar stone, that came from Lipscomb County, Tex., and adjacent Ellis County, Okla. Similar blades and scrapers are also found in southern Kansas, north of this Texas-Oklahoma district in what has been called the Province of Quivira (Brower, 1898, 1899), in fact large blades of this type have been called the Quivira Blade. Throughout this general area are large deposits of gray chert where much material was quarried by the Indians and the present specimens may have come from there. That is old Wichita country and on the basis of a fifteenth-century date it is possible that the implements may indicate the presence of hunting parties from that tribe in this New Mexican area. In his listing of typical Wichita artifacts, however, Sayles (1935) does not include such blades and scrapers; hence they may have belonged to some other group. Such caches are not uncommon in areas farther east and north but, as far as evidence in the literature is concerned, seem to be rare in this district. A similar series of blades is reported to have been found about 10 miles (16.1 km.) south of the present location. They were not seen by any of the field party and the occurrence has not been verified. That these blades were actual implements and not blanks intended for further refinement into more specific tools is demonstrated by the secondary chipping along some of the edges and a certain amount of polish, in some areas on their surfaces, such as is acquired through use. Implements of this type were employed in the preparation and dressing of skins, particularly those from the buffalo. The snub-nosed and side scrapers in the series are of the types usually found in a hunting complex, although as a group the sizes are larger than similar tools from the basin and buried sites in the plain.

The fire pit, measuring 2 feet (61.0 cm.) by 3 feet (91.4 cm.), had no lining. It contained charcoal, ashes, splinters and fragments of charred bone, several vertebrae, one of which showed the effects of fire, and a calcaneum. The vertebrae and calcaneum are from the American antelope or pronghorn (*Antilocapra*).<sup>6</sup> There was an additional fire pit nearby, and a few bones from modern bison<sup>7</sup> were found in the vicinity, but no other cultural material was recovered.

### MOLLUSKS

Numbers of mollusk shells were found in the digging, and in order that there would be sufficient material for comparative purposes, specimens were collected from typical wet-weather lakes in the area surrounding the site. Others were gathered from shallow depressions where sand and surface soil had been blown out by wind action. These shells were sent to Dr. Frank C. Baker, University of Illinois, who reported that the collection contained a number of land and fresh-water species. Commenting on the collections Dr. Baker writes:<sup>8</sup>

The species of *Helisoma* from the pits and fossil deposits are the same as those living in the Recent fauna; none are extinct, as is the case among some of the vertebrates. The other species of land and fresh-water mollusks are also the same as typical members of the Recent fauna. This difference in geological faunal contents has been observed in many other places and is to be noted especially in some Pleistocene deposits where the mollusks show little change in form while the vertebrates, principally the mammals, contain several species now extinct.

It is interesting to note, although there may be no particular significance in the fact, that all the shells from the excavations around the basin are from a single, fresh-water species (*Helisoma tenue sinuosum* Bonnet) common in New Mexico, Arizona, Texas, and northern Mexico. Dr. Baker states that the form is "Usually named *tenuis* but it is a distinct race of the typical *tenuis* which is confined to Mexico, the types being described from the vicinity of the City of Mexico." The fact that the material from the basin represents a fresh-water species is additional corroboration for its having been a lake or series of ponds.

<sup>6</sup> Identified by Dr. David H. Johnson, assistant curator, division of mammals, U. S. National Museum.

<sup>7</sup> Bones identified by Dr. C. L. Gazin, assistant curator, division of vertebrate paleontology, U. S. National Museum.

<sup>8</sup> Letter to Dr. Paul Bartsch, curator, division of mollusks, U. S. National Museum.

Samples from the deposits representing the bottoms of the various filled-in ponds were examined for fossil diatoms by Paul S. Conger, custodian, section of diatoms, United States National Museum. None were found, however, and no help toward determining the age of the deposits was obtained from this possible source of information.

### SUMMARY AND DISCUSSION

From excavations on the northern rim of the Staked Plains, the brakes below, and the plain of the Canadian River valley south of the town of San Jon, N. Mex., came an interesting sequence of projectile point and other artifact types that sheds some light on the aboriginal occupation of that portion of the Southwest. Faunal associations and geologic horizons give good indication of relative age, but more evidence is needed before an actual chronology can be suggested. The investigations to date tend to corroborate implications observed in finds made elsewhere, particularly with respect to the relationship between certain kinds of projectile points, yet do not furnish the complete and detailed evidence essential to a thorough understanding of developments in the earlier stages of the lithic industries in the western Plains. Later types of stone tools and implements probably were made by Indian groups known to have hunted over that area. On the basis of present knowledge, however, it is not possible to assign specific forms to definite peoples. There unquestionably was a mixing of materials in late times when various bands swept back and forth across the region, following the great herds of bison, camping at the same water holes, and otherwise making use of the same territory. Until sites attributable to occupancy by single groups have been worked and the character of the artifacts made and used by them is established to the extent that they are readily recognized the identification of different objects in a mixed series as the product of a definite tribe is not feasible. The best that can be done is to suggest certain probabilities.

The oldest horizon in the district is represented by one type of projectile point occurring in association with the bones of an extinct species of bison and coming from a stratum in which mammoth bones and teeth also are present. The point is of a type that might be called Indeterminate Yuma, but in order to clarify a confusing situation with respect to that classification it is designated the San Jon point. Indications are that it may be contemporaneous with the Folsom horizon, one of the oldest thus far established, but more

satisfactory evidence is necessary to establish that fact. In some ways this type of point is quite like others found under somewhat similar circumstances, points also identified as Indeterminate Yuma, that apparently have a late contemporaneity with Folsom types and that persisted after the latter were no longer made (Roberts, 1940, pp. 64-65). Hence it is possible that this early San Jon level dates from the closing stages of the Folsom horizon, some 10,000 to 15,000 years ago. Geologic studies tend to substantiate such a conclusion, although it must be regarded as tentative until more work has been done on that particular phase of the problem.

The next oldest remains comprise an assemblage of modern bison and deer bones and points of the Collateral or Eden Valley Yuma type. The significant factor in connection with this horizon is that geologic evidence demonstrates that between it and the preceding occupation there was a lengthy period of erosion followed by another during which there was considerable deposition of new material. The time lapse indicated is a relatively long one and during the interval the large bison were replaced by a smaller species, the modern buffalo. The cultural material from this level is unquestionably much younger than that from the underlying one, a fact that has important implications with respect to the status of different types of projectile points in the Yuma series. There has been a general tendency to regard all forms of the Yuma as more or less contemporaneous and indicative of the same cultural age. If the San Jon point from the oldest level is considered as an example of the Indeterminate Yuma, a questionable classification discussed in the detailed consideration in preceding pages, it is obvious that at least two of the Yuma forms occurred in sequence and are characteristic of chronologically different stages. The present evidence tends to support a previous suggestion to the effect that some of the generalized points regarded as Indeterminate Yuma may represent the form out of which the true Yuma developed. The definite break in occupation between the two levels here, however, shows that the transition did not take place in the San Jon district but if it actually did occur was accomplished elsewhere.

The break in occupancy evinced by the nature of the deposits is of interest because it is in accord with indications noted in other areas. For some as yet unexplained reason at most sites where traces of the earliest hunting cultures now recognized are found there is a definite hiatus between them and the following stages. Whether there actually was an interval during which the regions where these mani-



festations occur were uninhabited or whether it was only the particular sites that were not lived on, the people camping elsewhere and leaving materials not yet properly identified, is a problem still to be solved. The consensus of many is that there was an actual interruption in the stream of migration flowing from the Old to the New World and that for a time vast stretches of the western Plains and the Great Basin were uninhabited; that the first peoples had pushed on southward and into Middle America, although traces of them have not yet been found there, and those who were following had not yet arrived. Others maintain that once man had reached the North American continent there was no break in the continuity of occupation, that the evidence just has not been found or else has not been recognized. There are places where an unbroken sequence from early to modern times is suggested (Sayles and Antevs, 1941), but there still is a question as to whether or not there is a gap between the beginning of that series and some of the other older forms. Perhaps the correct conception is that in some districts remnants of the early migration persisted and ultimately were joined by incoming groups of a later movement, while in other sections the dispersal of peoples into the more southerly regions left large areas unoccupied sufficiently long for natural agents to cover their former camping places before others drifted in and settled at the same locations. Such certainly seems to have been the case at San Jon.

From the appearance of the Yuma type points down to late proto-historic times there was no break in the occupation of the area investigated. Projectile points progress through forms similar to some of those found in the Texas area to the east to the small, notched types associated with late sites in many parts of the country. Accompanying these are stone implements of the kinds that normally occur in the complex of hunting or hunting-seed-gathering peoples. In addition the material from the latest level contained potsherds. Among the stone objects are forms similar to those that have been attributed to the Wichita and the Jumano Indians, others that are like artifacts from sites in the Panhandle district along the Canadian, and still others that can be duplicated in material coming from eastern Pueblo ruins. The potsherds are of two types, one a buff or brownish-colored ware similar to that occurring in house ruins along the Canadian River that probably belongs to the broad, basic type represented in the wares of the Jumano and the Wichita, that have some relationship to those of the Caddo, and the other a black-on-white ware that was derived from a Pueblo type. The latter, called Chupadero Black



on White, is commonly found with brown wares such as those in the San Jon collection, and is a form that was taken over bodily, becoming a part of the ceramic complex of the brown-ware-making peoples. Considered as a whole, the series of implements from the late horizon definitely indicates that several different Indian groups used that area as hunting territory, a fact that is borne out by historical documents of later times.

On the basis of geologic studies and the presence of certain types of Pueblo potsherds in deposits at other locations in the district, supplemented by the evidence of the Chupadero Black on White at the basin site, the period of the last horizon is judged to be in the late fourteenth or early fifteenth century. Even with full allowance for an appreciable interval for the intervening point types, the period of the Collateral or Eden Valley Yuma is much later than has generally been supposed. If the San Jon point horizon is approximately of the age suggested, the gap between the two is indeed a broad one. Subsequent work on the geology may show that the deposits containing the San Jon point and extinct species of animals is more recent than indicated at present, but the break in the sequence would still be of sufficient proportions to cast doubt on the idea of a continuity of peoples in the area.

In general it may be said that the remains in the San Jon district are those of a hunting and hunting-seed-gathering peoples whose closest affinities were with the Plains cultures. Such traits as are suggestive of the Pueblo pattern to the west were either borrowed or are present because of trade relations. Pueblo peoples on occasion did get that far east, as is shown by sporadic finds along the Canadian and in later times by historical records, but apparently did not linger long enough to have any marked effect on the archeological picture. The earliest occupants of the region depended on the large bison for subsistence, while later groups hunted buffalo, deer, and antelope, and gathered the native food plants.

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1. VIEW OF THE NORTH RIM OF THE STAKED PLAINS

Photograph by Edison P. Lohr.



2. MAIN ARROYO

Line of old lake bottom can be seen along top of light-colored earth.  
Expedition camp at left.



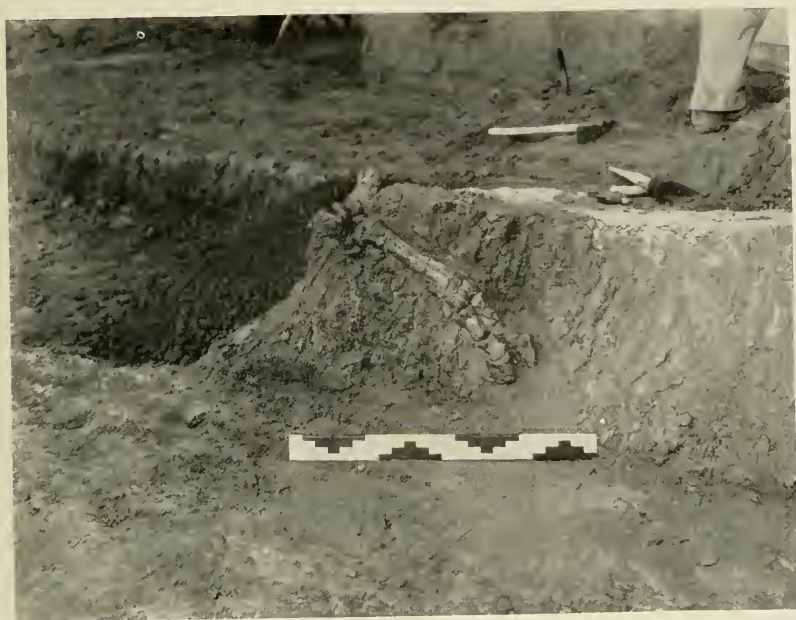


1. STARTING EXCAVATION IN ONE OF THE ARCHEOLOGICAL AREAS



2. MASS OF BISON BONES AT BOTTOM OF ONE OF SECTIONS





1. BISON FOOT AND LOWER LEG BONES IN SILT LAYER AT BOTTOM OF FORMER POND



2. OCCUPATION LEVEL EXPOSED IN ARROYO BANK IN LOWER PLAIN  
Workman pointing to hearth.



ARROWHEADS, SNUB-NOSED SCRAPERS, AND POINTS FROM KNIFE BLADES

(Actual size.)

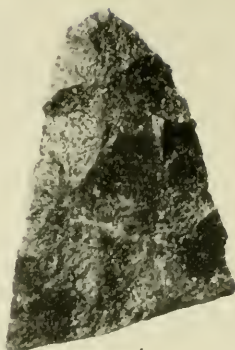


SCRAPERS AND ROUGH FLAKE KNIVES  
(Actual size.)





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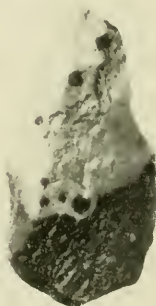
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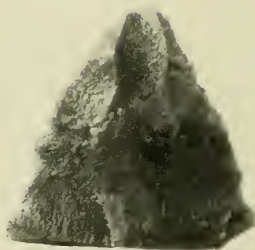
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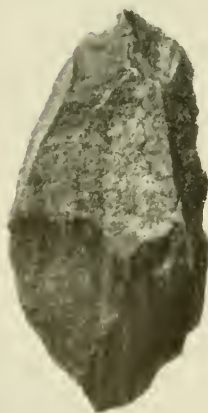
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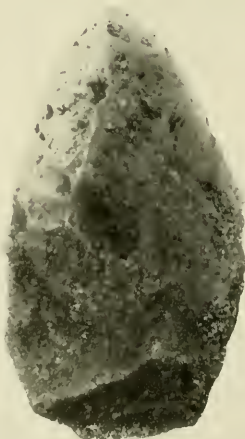
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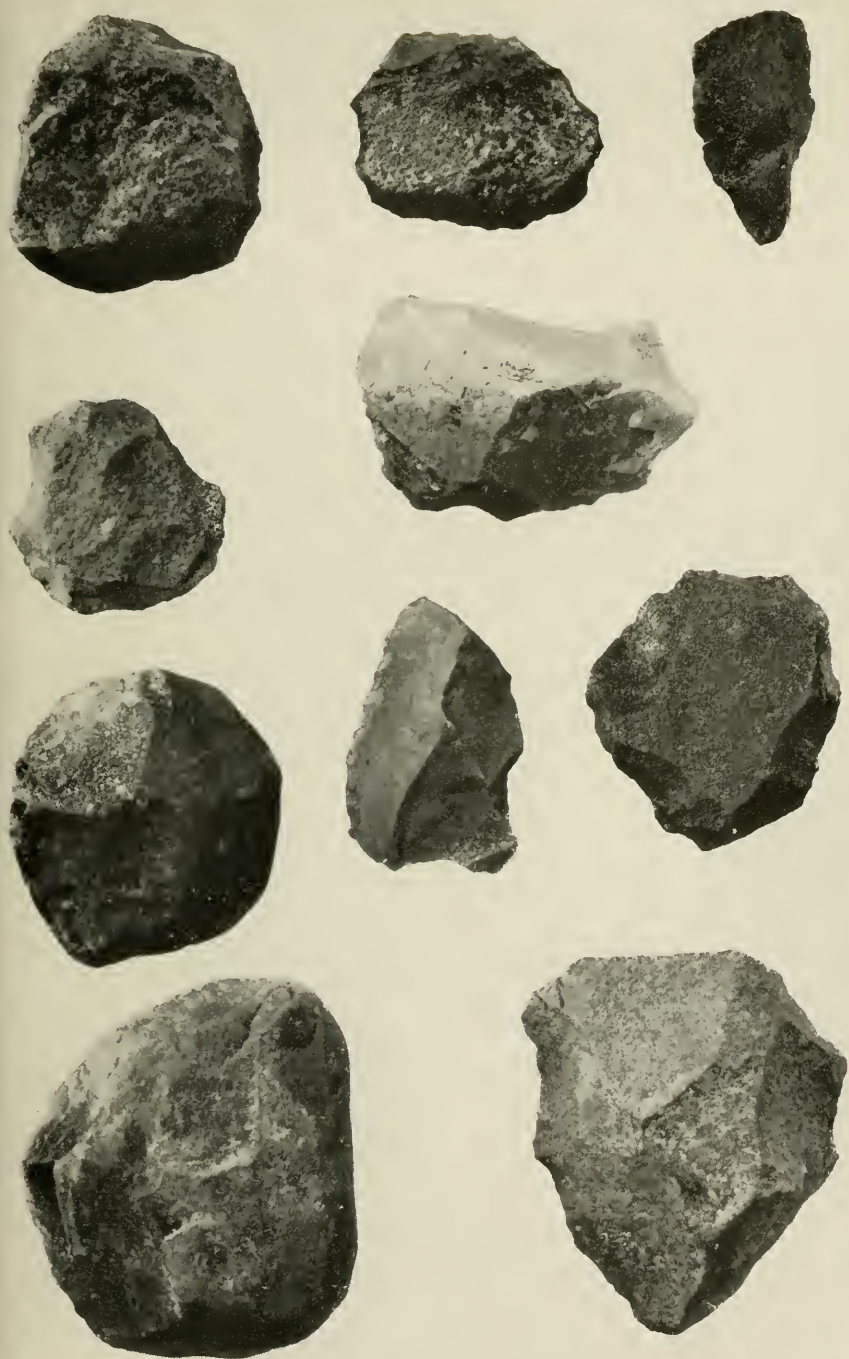
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CHOPPERS AND HAND HAMMERS  
(One-fourth actual size.)





LARGE BLADES FROM CACHE IN LOWER PLAIN



SCRAPERS AND FLAKE KNIVES FROM CACHE IN LOWER PLAIN  
(One-fourth actual size.)









SMITHSONIAN MISCELLANEOUS COLLECTIONS  
VOLUME 103, NUMBER 5

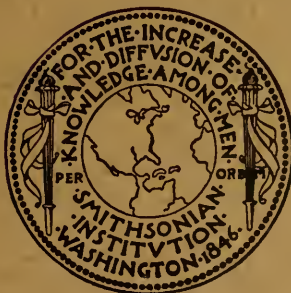
# NEW UPPER CAMBRIAN TRILOBITES

(WITH 21 PLATES)

BY

CHARLES E. RESSER

Curator, Division of Invertebrate Paleontology and Paleobotany  
U. S. National Museum



(PUBLICATION 3693)

CITY OF WASHINGTON  
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# NEW UPPER CAMBRIAN TRILOBITES

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(WITH 21 PLATES)

## INTRODUCTION

Soon after 1878 when Dr. C. D. Walcott centered his main efforts on the study of the Cambrian system, he conceived the idea of a monograph series, each of which should contain descriptions of all Cambrian fossils representing a major animal group. With this in mind he published new genera from time to time, frequently accompanied by descriptions of only one species, because the others were left for the monograph. Thus, for example, brachiopod genera were established and in 1912 the monograph of this group appeared. Likewise trilobite genera were described with the view of producing such a monograph in due course. For this reason practically all the genera then known from the older beds were described in 1891.<sup>1</sup>

By 1920 it was clear that a monograph by him on Cambrian trilobites, like that on the brachiopods, was not feasible. Nevertheless he continued segregating specimens and in 1924 and 1925 published more generic descriptions.<sup>2</sup> In the two years remaining before his death in 1927 Dr. Walcott set aside some of the specimens here presented, and less than 2 weeks before his passing he urged me to carry on and describe species as rapidly as possible so that they would become available for use.

Since 1925 there has been increased activity in the study of Cambrian geology. Numerous papers describing many new genera have

<sup>1</sup> Walcott, C. D.:

1891. Fauna of the Lower Cambrian or *Olenellus* zone. 10th Ann. Rep. U. S. Geol. Surv. 1891, pp. 507-774.

1916. Cambrian trilobites. Smithsonian Misc. Coll., vol. 64, No. 3, pp. 157-258, pls. 24-38.

1916. Cambrian trilobites. Ibid., vol. 64, No. 5, pp. 303-456, pls. 45-67.

<sup>2</sup> Walcott, C. D.:

1924. Cambrian and Lower Ozarkian trilobites. Smithsonian Misc. Coll., vol. 75, No. 2, pp. 53-60, pls. 9-14.

1925. Cambrian and Ozarkian trilobites. Ibid., vol. 75, No. 3, pp. 61-146, pls. 15-24.

appeared, but in most cases they also included only one or two species in addition to the genotype. This situation leaves many of the genera inadequately portrayed and also fails to make available the species needed for stratigraphic purposes. Hundreds of undescribed species contained in the National Museum collections need to be described, both to improve the concept of genera and to supply species for stratigraphic work. Many of them cannot appropriately be included in faunal or regional studies and are therefore best described in papers of this type.

Only a few of the genera represented by species described in this paper can be referred to higher taxonomic categories. It would be a simple matter to assign old family names or apply new ones to genera that bear superficial resemblances to one another, but such action would perpetuate existing errors and introduce new ones. Trilobites cannot yet be satisfactorily classified, and to attempt to do so merely adds to the confusion now existing.

#### DESCRIPTION OF GENERA AND SPECIES

##### KOMASPIDAE Kobayashi, 1935

Kobayashi established this family to include *Komaspis* Kobayashi, *Chariocephalus* Hall, *Irvingella* Ulrich and Resser, *Irvingelloides* Kobayashi, and *Bathynotus* Hall. Komaspidae was a poor selection as the family name, for both *Chariocephalus* and *Irvingella* are far more characteristic of the family than the obscure *Komaspis*. More than 50 species of *Chariocephalus* and *Irvingella* now studied show that the genotype of *Chariocephalus* is nowhere near the median point of the generic limits, and that *Chariocephalus*, *Irvingella*, and several other genera intergrade to the extent that arbitrary lines of separation must be drawn. No question regarding family relationships of these two genera can be raised, but there is no certainty that they belong with *Komaspis*.

Why Kobayashi should have assigned *Bathynotus* to this family, even tentatively, is difficult to understand. It was evidently done because of its large eyes, but there is not the remotest relationship with the Komaspidae expressed thereby.

In 1938 Kobayashi added *Dartonaspis* Miller to the family, at the same time erecting two subgenera, *Irvingellina* and *Parairvingella*, which are discussed on a later page. Also, he added the genus *Komaspidella* based on *Agraulos* (?) *thea* Walcott. The latter species, however, is a *Kingstonia* and therefore belongs in a different family. The type of *Dartonaspis* belongs to *Chariocephalus*, and hence this name becomes a synonym.

On the other hand the subgenus *Parairvingella*, based on *Chariocephalus* (?) *tumifrons* Walcott (not Hall and Whitfield) deserves generic rank. Kobayashi's other subgenus *Irvingellina* based on Hall and Whitfield's species falls in *Irvingella*, as subsequently discussed.

It is doubtful whether *Irvingelloides*, which is based on a single incomplete cranidium, belongs in the family. The new genus, *Drumaspis*, is added to the family Komaspidae.

The family Komaspidae is characterized by a large, more or less quadrate glabella which extends almost the full length of the cranidium. Occipital furrow is deep and wide, and three pairs of glabellar furrows are usually developed. The real pair, generally deep, may or may not be interrupted in the center, and the next pair, if visible, consists of short lateral indentations while the anterior pair is always faint and situated far forward. Fixigenes essentially confined to palpebral lobes. Brim narrow, usually simple, but may have a narrow rim. Eyes large, in some species longer than the glabella. Librigenes usually rather narrow. Pygidium has a wide well-segmented axis; pleural lobes fused, pleural furrows deep. Border flattened or concave.

I recently discussed the relation of *Chariocephalus* and *Irvingella*, but now that many more species are determined, further remarks will be in order. As the matter now stands this family contains the following genera.

#### **Komaspis Kobayashi, 1935**

Glabella subconical; brim concave with slight rim; eyes moderate in length; anterior fixigenes developed.

Middle Cambrian, Asia.

#### **Chariocephalus Hall, 1863**

Glabella quadrate or expanded slightly forward; brim a simple bar; eyes moderately to extremely long; librigenes large; anterior fixigenes reduced or absent.

Upper Cambrian (upper Franconia zones), North America.

#### **Irvingella Ulrich and Resser, 1924**

Glabella quadrate to subconical; eyes always large; anterior fixigenes present; brim simple or slightly rimmed; librigenes very narrow; pygidium like *Chariocephalus*.

Upper Cambrian (lower and middle Franconia zones), North America.

**Parairvingella Kobayashi, 1938**

Glabella subconical to quadrate; eyes moderately large; brim concave, with rim and preglabellar area; anterior fixigenes present.

Upper Cambrian (Franconia zones), Nevada and Novaya Zemlya.

**Drumaspis, new genus (genotype, *D. walcotti*, new species)**

Glabella quadrate or subconical; eyes smallest in family; brim always has well-developed rim; anterior fixigenes very narrow, relatively wide rearward.

Upper Cambrian (middle Franconia zones), North America.

**CHARIOCEPHALUS HALL, 1863**

*Chariocephalus* HALL, 16th Ann. Rep. New York State Cab. Nat. Hist., p. 175, 1863; Trans. Albany Inst., vol. 5, p. 165, 1867.—ZITTEL, Handbook Pal., Bd. 2, p. 603, Munich, 1885.—MILLER, N. A. Geol. Pal., p. 538, 1889.—GRABAU and SHIMER, N. A. Index Foss., vol. 2, p. 279, 1910.—RESSER, Smithsonian Misc. Coll., vol. 97, No. 10, p. 28, 1938.

*Dartonaspis* MILLER, Journ. Pal., vol. 10, No. 1, p. 29, 1936.

Now that a large number of species is available, the distinction between *Chariocephalus* and *Irvingella* disappears, for the gap between the genotypes is bridged by a series of species, so that it becomes necessary to draw an arbitrary line of separation. As the line has been drawn in this paper, *Chariocephalus* occupies a slightly higher stratigraphic position than *Irvingella*, and thus far the two genera have not been found together at any locality. The stratigraphic position of *Chariocephalus* seems to be in the beds of upper Franconia age.

In view of the arbitrary separation now necessary between *Chariocephalus* and *Irvingella*, a new generic diagnosis is presented, taking into account the features added by study of the many additional species. It will be noted that the relative size and position of the eye has become a less diagnostic criterion.

*Chariocephalus* is characterized by its very large, essentially quadrate glabella that occupies nearly the full cranial length. It may be slightly expanded forward, and in rare instances constricted near the midpoint. Anterior angles are usually well rounded, and the front outline may be gently curved, straight, or even slightly indented. If present on the outer surface, the glabellar furrows are wide and shallow, but most exfoliated specimens show three pairs of prominent furrows. The rear pair may be united but usually is interrupted. If present, the third pair is situated so far forward that the short depressions arise from the rounded anterior angles. Dorsal furrow usually deep and wide even on the outer surface. A wide occipital furrow is



apparently visible on most unexfoliated cranidia. Occipital ring heavy and of nearly even width throughout. Brim consists of a simple bar of even width throughout, and never as long as the glabella is wide. It may be somewhat thickened and has various attitudes with respect to the horizontal plane. Eyes always very large, strongly bowed, and set off by a clearly defined palpebral furrow. Fixigenes confined to the large palpebral lobes between the eyes and dorsal furrow. Because the eyes usually extend far forward, they continue part way around the anterior angles. At the rear they may extend behind the ends of the occipital furrow, but if not, only very narrow and short postero-lateral limbs are formed.

Libragenes narrow and long. Ocular platform narrow, long, and curved somewhat less than the eye. Outer rim usually clearly defined, increasing in width toward the genal angle. Genal spines present. They vary from short to long slender spines several times the cranidial length. They are usually directed outward at a considerable angle to the axis. Some Wisconsin species, however, appear to have long curved genal spines which cross over the thorax to the extent that their outer extremities overlap.

Hypostoma nearly circular in outline, large, and characterized by a large central lobe. The alate portions are upturned toward the edges.

Pygidium ovate, with about half the area of the cranidium. The well-segmented axis is wide and long but tapers little. From two to four rings are defined and the terminal lobe may have faint impressions of others. The pleural platforms are convex, usually less than half the axial width at the same point, and drop off into a narrow flattened border.

Surface smooth.

*Genotype*.—*C. whitfieldi* Hall.

The fragment described by Raymond as *Chariocephalus peloris* (Bull. Geol. Soc. Amer., vol. 48, No. 8, p. 1119, pl. 3, fig. 12, 1937) is excluded from the genus by its small eye, and the direction and depth of the glabellar furrows.

As stated above, Kobayashi's *Irvingella* (*Irvingellina*) *protuberans* (Jap. Journ. Geol. Geogr., vol. 5, Nos. 3-4, p. 176, pl. 15, figs. 1a-c, 2, 1938) falls into *Chariocephalus*.

#### CHARIOCEPHALUS TENERUS, new species

##### PLATE I, FIGURES 1-3

This moderately small species, represented by a single almost entirely exfoliated cranidium, is the only example of the genus found in this collection.

The glabella is slightly expanded and the anterior angles are rounded off. Because it is exfoliated, the three pairs of furrows show clearly, the wide posterior pair continuing across the glabella. On the test this glabellar furrow is very shallow and possibly interrupted in the middle. The brim is of moderate width and slightly upturned. Exclusive of the wide dorsal furrow the palpebral lobes, which also are the fixigenes, are nearly half the width of the glabella and maintain most of their width to the occipital furrow. The eyes measured in a straight line from end to end are almost as long as the glabella and, of course, measured around their outer edge are longer than that. The eyes extend from the occipital furrow to a point about one-sixth the width of the glabella beyond the lateral dorsal furrow. This leaves a narrow fixigene slightly exceeding the width of the eye band at the forward end of the eye. The glabella is rather evenly convex both laterally and longitudinally, with a moderate curvature. As can be seen in the front view, the librigenes are rather sharply and evenly curved, first rising considerably above the bottom of the dorsal furrow.

Honey Creek limestone; (loc. 37t) 4 miles southeast of Hennepin, Arbuckle Mountains, Oklahoma.

*Holotype*.—U.S.N.M. No. 108631.

#### CHARIOCEPHALUS BELLUS, new species

##### PLATE I, FIGURES 4-6

This species, represented by cranidia only, is associated with *C. bulla*.

*C. bellus* is characterized by its quadrate glabella. Although the front of the glabella and the anterior angles have the aspect of a quadrate form, the illustration shows that both are definitely rounded. In addition to the occipital furrow, there are the usual three pairs of glabellar furrows, the posterior pair being connected across the middle by a faint depression while the anterior pairs are very shallow throughout. Brim convex and turned down slightly. The fixigenes at their widest point are about one-third the width of the glabella. The exceedingly long eyes extend forward well beyond the lateral dorsal furrow. The glabella is evenly convex laterally. It is highly convex longitudinally, the curvature being concentrated in the forward third. The fixigenes are only slightly curved in cross section and slope down from the relatively shallow dorsal furrow at about the same angle as the lateral slopes of the glabella. Surface punctate.

Honey Creek limestone; (loc. 37v) West Timbered Hills, Arbuckle Mountains, Oklahoma.

*Holotype*.—U.S.N.M. No. 108632.

**CHARIOCEPHALUS BULLA, new species**

## PLATE I, FIGURES 7-11

Several cranidia and a pygidium are placed in this moderate-sized species. *C. bulla* is a large-eyed form and hence resembles *C. bellus* and *C. tenerus*.

The glabella is essentially quadrate, with rather strongly marked furrows on the exfoliated holotype. The anterior outline is nearly straight between the broadly rounded anterior corners, and the narrow brim is only slightly thickened. Fixigenes are confined to the palpebral lobes and at their widest point are a little less than half the width of the glabella. The long eyes do not reach the posterior furrow, and in front, they end exactly at the outer edge of the dorsal furrow, and hence are relatively shorter than in *C. bellus* or *C. tenerus*. The glabella is convex laterally with the greatest curvature near the dorsal furrow. Longitudinally the greatest curvature is toward the anterior end. Fixigenes are considerably curved and slope downward from the moderately deep dorsal furrow. The pygidium is somewhat narrow and rather convex, with the axis standing wholly above the pleural lobes. As a whole the pygidium slopes rearward at a moderate rate, terminating with an abrupt slope. In fact, the rear end of the axis slightly overhangs the border. The pleural lobes form triangular platforms that drop off to the slightly flattened border, which becomes rather narrow at the rear of the axis.

Honey Creek limestone; (loc. 37v) West Timbered Hills, Arbuckle Mountains, Oklahoma.

*Holotype*.—U.S.N.M. No. 108633a; *paratype*, No. 108633b.

**CHARIOCEPHALUS TERES, new species**

## PLATE I, FIGURES 12, 13

This large-eyed species, resembling *C. tenerus*, is represented by a few cranidia, none of which is complete. The illustrated holotype is partially exfoliated and the anterior portion of the glabella abraded.

The glabella is somewhat ovate, owing more to the rounded front margin and rounded anterior angles than to the slight constriction toward the rear. The furrows are developed normally but may be fainter than the average species from the region. Incomplete preservation prevents an exact description of the brim but it seems to be wide and slightly upturned, though not thickened. The fixigenes are nearly half the width of the glabella. Eyes are very long, extending from the occipital furrow well beyond the lateral course of the facial suture, and therefore exceed the glabella in length. Surface punctate.

Honey Creek limestone ; (loc. 37v) West Timbered Hills, Arbuckle Mountains, Oklahoma.

*Holotype*.—U.S.N.M. No. 108634.

**CHARIOCEPHALUS AFFINIS**, new species

PLATE 1, FIGURES 14-20

This species, represented by a number of examples of all parts, is perhaps most closely allied to *C. bulla*.

The glabella is well rounded at the anterior angles, but has parallel sides and only two pairs of furrows. It is convex, having an even curvature laterally, but longitudinally its greatest curvature is in the anterior third. The nearly flat fixigenes, a little more than a third the width of the glabella at their widest point, slant downward from the shallow dorsal furrow at a smaller angle than the lateral slope of the glabella. The eyes are long, extending forward beyond the lateral dorsal furrow. An associated librigena and a pygidium are assigned to this species. The pygidium is transverse and the axis does not rise wholly above the pleural lobes. The pleural lobes form very narrow platforms, which are elongate rather than triangular, and which slope into a broad concave border with a thickened, slightly upturned rim.

Honey Creek limestone ; (loc. 37u) West Timbered Hills, Arbuckle Mountains, Oklahoma.

*Cotypes*.—U.S.N.M. Nos. 108635a-c.

**CHARIOCEPHALUS AGRARIUS**, new species

PLATE 1, FIGURES 21-28

In present collections this moderately large-eyed form is the most common *Chariocephalus* species at the locality. It is represented by all cranidial parts and the pygidium.

The wide glabella expands only slightly, standing entirely above the fixigenes. It is very convex laterally, with a slightly flattened profile. Longitudinally it is also strongly convex, with the greatest amount of curvature in the front half. The front outline is rounded, and the dorsal furrow is relatively shallow. The brim is very slightly thickened and is turned up to a nearly horizontal position. The fixigenes at their widest point are nearly half the width of the glabella. The eyes extend from a short distance forward of the occipital furrow to the dorsal furrow. Exfoliated specimens show normal depth for glabellar furrows. The fixigenes are only slightly convex and slope down from the rather broad and shallow dorsal furrow. Distinct pits are developed at the anterior angles in the dorsal furrow. The libra-

gene selected for this species is of ordinary shape and dimensions. The rarely found hypostoma is here preserved. It is characterized by a tumid central lobe and a relatively narrow upturned alate portion.

The pygidium assigned to the species has a wide axis with three well-defined rings, and stands completely above the pleural platforms. Pleural lobes form an elongate platform which slopes abruptly to the horizontal, slightly thickened border.

Honey Creek limestone; (loc. 37v) West Timbered Hills, Arbuckle Mountains, Oklahoma.

*Holotype*.—U.S.N.M. No. 108636a; paratypes, Nos. 108636b-e.

#### CHARIOCEPHALUS ANGUSTATUS, new species

PLATE I, FIGURES 35-40

This is one of the smaller species and in several respects approaches closer to the genotype than most Oklahoma forms. It is represented by several cranidia, together with a pygidium assigned to it.

The slightly expanded glabella is rather long and has three pairs of furrows visible. It is highly arched transversely. Longitudinally it stands completely above the fixigenes, but the convexity in that direction is confined almost entirely to the anterior fourth. The occipital furrow is exceptionally wide and deep. The brim consists of a simple bar. Pits are present at the anterior angles in the dorsal furrow, which is wide but not as deep as usual. The fixigenes are considerably less than half the glabellar width, and are flatly convex, as a whole sloping only slightly downward from the dorsal furrow. Rather long eyes are bowed most strongly anterior to the middle of the glabella, which causes the species to have the aspect of the genotype.

The associated pygidium assigned to the species has a moderately high axis and relatively narrow pleural platform. The border is also relatively narrow with slightly thickened edge.

Honey Creek limestone; (loc. 37v) West Timbered Hills, Arbuckle Mountains, Oklahoma.

*Holotype*.—U.S.N.M. No. 108637a; paratype, No. 108637b.

#### CHARIOCEPHALUS GRACILENS, new species

PLATE I, FIGURES 29-31

This is the smallest species in the Wichita Mountains collections, and as far as brim structure is concerned conforms rather closely to the genotype.



The glabella is quadrate, being rounded slightly at the anterior corners. The dorsal furrow is wide and rather deep and has pits at the anterior angles. The occipital furrow is wide and deep, but the glabellar furrows are faint, the rear pair showing only as faint depressions. The fixigenes are slightly less than half the width of the glabella. The eyes extend far forward, terminating about a half millimeter behind the dorsal furrow pits. The brim consists of a slightly thickened narrow bar.

Honey Creek limestone (*Ptychaspis* beds); (loc. 9y) 2 miles southeast of Canyon Creek, Wichita Mountains, Oklahoma.

*Holotype*.—U.S.N.M. No. 108638.

#### CHARIOCEPHALUS MONTIS, new species

PLATE 1, FIGURES 32-34

Only a few cranidia of this small species have been located.

The glabella is practically rectangular in outline with the anterior corners rounded. In the exfoliated holotype the furrows are so shallow that they presumably did not show on the exterior surface. The brim consists of a rather stout, slightly thickened bar. The dorsal furrow is wide and fairly deep. The fixigenes at their widest point are a little more than one-third the glabellar width, while the anterior fixigenes are about as wide as the eye band. The eyes are very long, extending from the occipital furrow to a point beyond the sides of the glabella, and are highly bowed with a fairly even curvature. The glabella is rather evenly curved laterally, and longitudinally the rate of curvature increases from the rear pair of the glabellar furrows forward. The fixigenes are rather flat, sloping slightly downward from the dorsal furrow.

Honey Creek limestone (*Ptychaspis* beds); (loc. 91q) 8 miles southeast of Mountain View, Wichita Mountains, Oklahoma.

*Holotype*.—U.S.N.M. No. 108639.

#### CHARIOCEPHALUS WICHITAENSIS, new species

PLATE 2, FIGURES 1-8

This is one of the larger species and is represented by several cranidia and other parts. The cranidium expands slightly and is rounded at the anterior corners to the straight front outline. In fact, the front of the glabella is slightly indented. The occipital furrow is deep, but only the rear pair of glabellar furrows shows on the exterior, while the other two pairs are faint on exfoliated specimens. The glabella stands above the level of the fixigenes and its convexity laterally is produced by a gently curving top and relatively steeply

sloping sides. Longitudinally the moderate convexity is practically confined to the anterior lobe. The brim consists of a narrow band in a slightly upturned position. The fixigenes at their widest point are about half the width of the glabella and the long eyes have a nearly circular curvature. They extend forward to the dorsal furrow and back practically to the occipital furrow. The narrow librigenae has a long, slender, straight genal spine which extends outward at a considerable angle to the axis. The pygidium is characterized by a wide tapering axis with three rings and terminal segment. Fusion has not entirely eliminated the pleural grooves. Pleural platforms narrow because of the long slope to the marginal furrow.

Honey Creek limestone (*Ptychaspis* beds); (loc. 91q) 8 miles southeast of Mountain View, Wichita Mountains, Oklahoma.

*Holotype*.—U.S.N.M. No. 108640a; paratypes, Nos. 108640b-e.

#### CHARIOCEPHALUS ULRICHI, new species

PLATE 2, FIGURES 9-14

This is another large and well-represented species, similar to *C. wichitaensis*. In fact the two are so similar that a formal description of this species is not needed. *C. ulrichi* differs in several respects, the most notable of which are the presence of a narrow anterior fixigene and greater curvature of the eyes so that the rear portion of the fixigene is relatively more contracted. The increased curvature of the eye is accompanied by a slightly greater relative width of the palpebral lobe making it equal to half the glabellar width.

The associated pygidium of *C. ulrichi* differs considerably from the others found in Oklahoma. Its axis slopes rearward into the dorsal furrow, which grows more shallow in the same direction, so that the rear portion of the axis merges into the pleural lobes. The whole pygidium slopes in all directions from the median point of the anterior axial segment.

Honey Creek limestone (*Ptychaspis* beds); (loc. 9y) 2 miles southeast of Canyon Creek, Wichita Mountains, Oklahoma.

*Holotype*.—U.S.N.M. No. 108641a; paratypes, Nos. 108641b-d.

#### CHARIOCEPHALUS MAGNUS, new species

PLATE 2, FIGURES 15-17; PLATE 12, FIGURE 13

This beautiful, large species is represented by the complete holotype and several imperfect cranidia.

The quadrate glabella is slightly constricted in its middle portion. It stands well above the fixigenes and is convex laterally, with a circular profile. Longitudinally the considerable convexity is confined

to the anterior third. The brim is not well preserved, but apparently narrow, with a slightly upturned edge. Fixigenes, confined to the palpebral lobes, at their widest point are less than half the width of the glabella. Anterior fixigenes wanting. The eye, with a nearly circular curvature, extends forward to the dorsal furrow. The palpebral lobes are flat for most of their width, but at the outer margins turn down very sharply so that their anterior portions actually bulge over the eye band. Dorsal furrow wide and deep on exfoliated cranidia, while the first pair of glabellar furrows are wide but shallow. Test smooth. Where partially exfoliated, the remaining thin portion of the test is finely punctate.

Lyell formation; (loc. 20j) Tilted Mountain Brook,  $9\frac{1}{2}$  miles east of Lake Louise, Alberta.

*Holotype*.—U.S.N.M. No. 108642.

**CHARIOCEPHALUS BADGERENSIS, new species**

PLATE 2, FIGURES 18-20

This species, represented by only a few cranidia, is about normal in size, and in general appearance approaches close to the genotype.

The glabella is quadrangular, with rounded anterior corners. Two pairs of glabellar furrows are faintly indicated, besides the exceptionally wide occipital furrow. Brim relatively wide with an upturned margin. Dorsal furrow wide and deep. Fixigenes at their widest point less than one-third the width of the glabella. Very narrow anterior fixigenes remain. Since the eye does not reach to the occipital furrow, fixigenes remain posterior to the eye and are about equal to one-fourth the glabellar width at that point. The eye extends from a point opposite the forward ends of the occipital furrow on the glabella to the dorsal furrow, and is rather sharply bowed. In longitudinal section the cranidium is moderately convex with the greater portion of the convexity concentrated in the anterior lobe. Laterally the glabella is rather evenly convex and the palpebral lobes moderately convex. Exfoliated surface punctate.

Lyell formation; (loc. 19u) Badger Pass, Johnson Canyon, 8 miles east of Lake Louise, Alberta.

*Holotype*.—U.S.N.M. No. 108643.

**CHARIOCEPHALUS BURLINGI, new species**

PLATE 2, FIGURE 21

This is the largest species of *Chariocephalus* found thus far. Although the material is hardly adequate as the basis of a species, yet its description is included because the fauna is very important for

stratigraphic reasons and further collecting is difficult. It is most closely related to *C. badgerensis*.

The incomplete holotype cranidium has a large quadrate glabella, slightly constricted in the middle. The occipital furrow is wide and deep but does not join the dorsal furrow with the same strength. No doubt on the outer surface of the test this furrow was either rather shallow or obscelescent toward its ends. The rear pair of glabellar furrows is somewhat less recurved than in *C. badgerensis*. The fixigenes at their widest point are equal to nearly half the glabellar width. In cross section the entire cranidium is somewhat flat, and the palpebral lobes slope gently from the dorsal furrow. The eyes appear to have been rather long but their anterior ends are not preserved. Both the test and the exfoliated portions are smooth.

Lynx formation; (loc. 190) Iyatunga Mountain, Robson Peak District, British Columbia.

*Holotype*.—U.S.N.M. No. 108644.

#### IRVINGELLA ULRICH AND RESSER, 1924

*Irvingella* ULRICH and RESSER, in Walcott, Smithsonian Misc. Coll., vol. 75, No. 2, p. 58, 1924.—WALCOTT, *ibid.*, No. 3, p. 98, 1925.—WALCOTT and RESSER, Rep. Sci. Results Norwegian Exp. Novaya Zemlya, No. 24, Vidensk., p. 10, Kristiania, 1925.—RESSER, Smithsonian Misc. Coll., vol. 97, No. 10, p. 33, 1938.

*Irvingellina* KOBAYASHI, Jap. Journ. Geol. Geogr., vol. 15, Nos. 3-4, p. 175, 1938.

Relationships between *Irvingella* and the other genera of the Komaspidae have been discussed. Kobayashi erected the subgenus *Irvingellina* on *Chariocephalus tumifrons* Hall and Whitfield. Although the brim of that species is not fully typical of *Irvingella*, owing to the upturned edge forming a rim, its essential structure remains that of a bar and therefore agrees in every respect with *Irvingella*. The other species that Kobayashi assigned to *Irvingellina* are referred as follows: *Irvingella arctica* Walcott and Resser to *Parairvingella*; *Irvingella gibba* Miller and *I. (Irvingellina) protuberans* Kobayashi to *Irvingella*.

Even though published descriptions of *Irvingella* are very brief, they continue to be adequate in spite of the addition of many new species.

*Genotype*.—*I. major* Ulrich and Resser, 1924.

#### IRVINGELLA SILVESTRIS, new species

##### PLATE 2, FIGURES 22-27

This average-size plump species is represented at several localities in the Arbuckle Mountains by numerous cranidia.

The wide glabella is constricted to a rounded anterior outline. The occipital and first pair of glabellar furrows are narrow, but clearly defined, and in exfoliated specimens the anterior pair is visible. The dorsal furrow is wide and deep. The glabella, slightly flattened on top, stands wholly above the fixigenes and the dorsal furrow on the sides while in front it overhangs that furrow. Longitudinally the head is highly convex, the glabella curving throughout has its greatest convexity in the anterior half. The brim is narrow, its position continuing the downward trend of the cranial curvature. At their widest point the fixigenes are a little more than one-third the glabellar width. They contract rearward from their widest point which is situated anterior to the middle of the head. Their anterior portion is about half their average width, but because of high convexity in dorsal view they appear much narrower. Laterally the fixigenes are considerably curved and like the glabella have the greatest curvature at the outer margins where they drop off to a wide palpebral furrow and eye band, which is practically horizontal. Longitudinally the fixigenes rise abruptly from the depressed posterolateral limbs, and then slope gradually until near the forward end of the eye, where they drop off abruptly to meet the depressed brim.

Honey Creek limestone; (loc. 89w) west side of the West Timbered Hills; and (loc. 12p) 4 miles east of Alpers, Arbuckle Mountains, Oklahoma.

*Holotype*.—U.S.N.M. No. 108645a; paratype, No. 108645b.

**IRVINGELLA ARBUCKLENSIS, new species**

PLATE 2, FIGURES 28-33

This is a very prolific species of average size. The glabella, normal in size and depth of furrows, is constricted toward the front. The dorsal furrow is relatively shallow, but the glabella is well differentiated in cross section because it stands completely above the fixigenes. Laterally the glabella is evenly curved, attaining a height equal to about one-half its width. In the opposite direction the considerable convexity is attained by declivity of the forward moiety. The brim, of normal width, slopes downward from the anterior furrow. The fixigenes are slightly less than half the width of the glabella; thus the eyes are set at a considerable angle to the dorsal furrow. They increase in width from front to back. The anterior portion is flexed downward into a nearly vertical position and so is much wider than appears in dorsal view. The eyes extend from about the occipital furrow forward only to the anterior glabellar furrow, and hence are



the shortest of any species observed. The anterior fixigenes are slightly abnormal owing to the presence of a shallow anterior furrow, which causes them to appear tumid in lateral section. Laterally the fixigenes are only slightly convex, except at their outer edges, and as a whole slope downward from the dorsal furrow. The eye band is upturned a little.

Honey Creek limestone; (loc. 89w) west side of the West Timbered Hills, Arbuckle Mountains, Oklahoma.

*Holotype*.—U.S.N.M. No. 108646a; paratypes, Nos. 108646b, c.

**IRVINGELLA MESLERI**, new species

PLATE 2, FIGURES 34-38

This average-size species is represented by a number of cranidia.

The long glabella decreases in width forward to the rounded anterior outline. Occipital and first pair of glabellar furrows deep; two other pairs visible. The dorsal furrow is wide and moderately impressed. The brim is rather wide and thick in the middle, and has a rimlike edge owing to the presence of an incipient anterior furrow. Fixigenes, at their widest point, nearly half the glabellar width. Their anterior portions, which are short owing to the fact that their greatest width occurs far forward, are about as wide as the rim and equally convex. The long eyes extend approximately from the occipital furrow to the brim. Laterally the fixigenes are only moderately convex and slope down slightly from the dorsal furrow.

Honey Creek limestone; (loc. 12n) 7 miles north of Springer, Arbuckle Mountains, Oklahoma.

*Holotype*.—U.S.N.M. No. 108647a; paratype, No. 108647b.

**IRVINGELLA RECURVA**, new species

PLATE 2, FIGURES 39-41

The glabella is rather wide and well rounded in front. The glabellar furrows are broad and deep, and the dorsal furrow is particularly wide and, in exfoliated specimens, also deep. In cross section the glabella stands completely above the dorsal furrow, and is flattened slightly on top. Longitudinally the rear third has a nearly straight profile, while the anterior portion bends down sharply to overhang the anterior dorsal furrow. The narrow brim is slightly thickened, and when viewed from the front has a sinuate outline. The fixigenes, which stand vertical, are only about one-fourth the width of the glabella. They are slightly convex and have considerable width in their anterior portions.

Honey Creek limestone; (loc. 12m) 7 miles north of Springer, Arbuckle Mountains, Oklahoma.

*Holotype*.—U.S.N.M. No. 108648.

**IRVINGELLA ALIA, new species**

PLATE 2, FIGURES 42-47

This species is represented by a few cranidia which are slightly above average size. The glabella is wide and rounded off at the anterior angles. All furrows are narrow but only moderately impressed. The glabella stands wholly above the dorsal furrow. Laterally it is rather convex with a nearly even curvature, but longitudinally the curvature extends from the rear margin to the front, increasing slowly for half the distance and then more rapidly. The brim is narrow and slightly thickened. Fixigenes narrow, being a little more than one-fourth the glabellar width. Their anterior angles turn down into a vertical position. Laterally the fixigenes are slightly convex, and slope down rather evenly from the dorsal furrow. The eyes are very long, extending from the occipital furrow to the brim.

Honey Creek limestone; (loc. 9p) about 15 miles northwest of Fort Sill, Wichita Mountains, Oklahoma.

*Holotype*.—U.S.N.M. No. 108649a; paratypes, No. 108649b.

**IRVINGELLA DAVISENSIS, new species**

PLATE 2, FIGURE 48

The genus *Irvingella* is very poorly represented in the Davis formation of Missouri, this being the only species that can now be described.

The glabella is rather narrow. The occipital furrow is wide and deep, but the glabellar furrows are shallow. Laterally the glabella is strongly convex, but not longitudinally. Brim is relatively wide and convex. The fixigenes at their widest point are more than half the width of the glabella at the same point. The anterior fixigenes are somewhat wider than the brim. They rise slightly from the dorsal furrow toward the eyes, then slope off gradually with increasing convexity toward the outer edges. The posterolateral limbs are sharply, and the anterior angles slightly, depressed. The eyes are of moderate length.

Davis formation; (loc. 22m) Shaw Branch, Davis Creek, Missouri.

*Holotype*.—U.S.N.M. No. 108650.

**IRVINGELLA OTTERTAILENSIS, new species**

## PLATE 2, FIGURE 49

One imperfect cranidium is available, but the species is described because of the importance of the fauna.

The glabella is rather large, with the occipital and first furrows sharply impressed, but the anterior pairs do not show. Convexity cannot be determined because of the partial compression of the fossils from this locality. The fixigenes are more than half the width of the glabella and the eyes are very long, extending from the occipital furrow around the sharply bowed cheeks to the brim.

"Goodsir" formation; Moose Creek, Ottertail Range, British Columbia.

*Holotype*.—U.S.N.M. No. 108651.

**IRVINGELLA OBLONGA, new species**

## PLATE 3, FIGURES 1-3

Although this locality has yielded numerous specimens of other *Irvingella*, only this cranidium of a small distinctly marked species was found.

The glabella is long and subcylindrical, well rounded in front. Its width equals about three-fourths its length. The occipital furrow and the complete rear glabellar furrow are both deep and approximately parallel. The glabella stands completely above the dorsal furrow, and in cross section has practically vertical sides rounding to the slightly flattened top surface. Longitudinally the high convexity is confined largely to the front half so that the anterior lobe overhangs the brim. Brim narrow and slightly upturned. Fixigenes about one-fourth the width of the glabella, retaining about that width throughout their length. The anterior portion decreases to about half the greatest width. The eyes are long and, because of the rather even width of the fixigenes, are not greatly bowed.

Wilberns formation; (loc. 70) Baldy Mountain, 8 miles northwest of Burnet, Texas.

*Holotype*.—U.S.N.M. No. 108652.

**IRVINGELLA AGRESTIS, new species**

## PLATE 3, FIGURES 4-6

The glabella tapers, owing to the even convergence of the dorsal furrow from the occipital furrow forward. The occipital and first

glabellar furrows are about equally deep and nearly parallel, and a faint second pair is present. Glabella stands completely above the fixigenes and is moderately and evenly curved laterally. Longitudinally there is considerable curvature which increases in amount from the occipital furrow forward. Brim of moderate width and development; only slightly thickened. Anterior fixigenes a little wider than brim. At their widest point they are about one-fourth the width of the glabella, decreasing in width toward the occipital furrow. Moderately bowed eyes extend forward nearly to the front end of the glabella.

Wilberns formation; (loc. 69) Honey Creek, 8 miles southeast of Llano, Texas.

*Holotype*.—U.S.N.M. No. 108653.

#### IRVINGELLA ARDMORENSIS, new species

##### PLATE 3, FIGURES 7-12

Only one comparatively large species of *Irvingella* occurs at this locality. An unusually wide variation in size has been allowed, for some crania are larger, while others are less than one-third the size of the specimens illustrated.

The glabella is nearly quadrangular in outline, tapering slightly forward to a rounded frontal outline in which there is a slight flattening medially. In cross section the glabella has considerable elevation produced by a fairly even curvature. Longitudinally it is also high, as shown by the illustrations. The glabellar profile shows a rise from the rear margin in a shallow curve to the front lobe of the glabella and then a very steep drop to the anterior furrow. Brim narrow and slightly thickened. Anterior fixigenes taper rapidly to the narrow brim, at their widest point being about one-third the glabellar width. The fixigenes have only a slight convexity. The eyes are a little more than half the length of the glabella and are only moderately bowed.

Honey Creek limestone; (loc. 12p) 4 miles east of Alpers, Arbuckle Mountains, Oklahoma.

*Holotype*.—U.S.N.M. No. 108654a; paratype, No. 108654b.

#### IRVINGELLA PLENA, new species

##### PLATE 3, FIGURES 13-15

This species, represented by numerous crania, is found in association with several other forms from which it is distinguished by its plumpness.

The cranium is nearly as wide as long and is well rounded off at the anterior corners. The second pair of glabellar furrows is fairly distinct although they fail to register in the photograph. In cross section the glabella is moderately high with a somewhat flattened top. Longitudinally its profile is rather straight in the rear, dropping off steeply in the anterior fourth. Brim of average width, slightly thickened and situated considerably below the dorsal furrow. Fixigenes very narrow; about the same width as the brim at the anterior angles, and at their widest point they equal about a fourth the glabellar width. They are rather highly arched so that they partly overhang the eye band.

Wilberns formation; (loc. 14b) Cold Creek, opposite north end of Sponge Mountain; (loc. 70) Baldy Mountain, 8 miles northwest of Burnet, Texas.

*Holotype*.—U.S.N.M. No. 108655.

**IRVINGELLA ALTA**, new species

PLATE 3, FIGURES 16-18

The wide glabella is only about a fifth longer than wide. The entire cranium is highly convex in both directions, with the posterolateral limbs depressed almost to a vertical position. The dorsal furrow is narrow. Three pairs of glabellar furrows are visible; both the occipital and the rear pair are relatively narrower and less deep than usual. Laterally the glabella is almost evenly curved, with a tendency toward forming a keel in the middle. The longitudinal profile is circular except in the anterior fourth where the curvature increases until the anterior glabellar lobe overhangs the brim. Brim narrow and compressed closely against the glabella. Fixigenes are less than a third the glabellar width and slope downward at a sharp angle from the dorsal furrow. The eyes are long and somewhat angulated at the widest point of the palpebral lobe. Surface of test evidently smooth.

Honey Creek limestone; (loc. 9p) about 15 miles northwest of Fort Sill, Wichita Mountains, Oklahoma.

*Holotype*.—U.S.N.M. No. 108656.

**IRVINGELLA DECKERI**, new species

PLATE 3, FIGURES 19-27

This species is represented by numerous cranidia. Specimens vary considerably in size, but their average is about that for the genus.

Taken as a whole the cranium has a more ovate shape than many other species. The large glabella is rounded in front. Dorsal furrow



shallow but clearly defined. Occipital furrow narrow. First pair of glabellar furrows continues across center unchanged in width but the anterior pairs are not visible. Laterally the glabella is moderately convex, with concentration of the greatest convexity near the center. Longitudinally the rear half is only slightly convex, but in the anterior portion the convexity increases until the slope becomes vertical. The brim is narrow and slightly thickened, sloping down from the anterior furrow. Fixigenes are about one-third the width of the glabella, their anterior portion measuring about one-third their average width. The eyes are as long as the glabella, extending beyond the line of the lateral dorsal furrow in front. The fixigenes slope downward rather evenly from the dorsal furrow.

Honey Creek limestone; (loc. 89y) West Timbered Hills, Arbuckle Mountains, Oklahoma.

*Holotype*.—U.S.N.M. No. 108657a; paratypes, Nos. 108657b, c.

#### IRVINGELLA BURNETENSIS, new species

PLATE 3, FIGURES 28-33

The cranidia representing this species are of average size and, as the illustrations show, are rather typical in form. The cranidium is subcylindrical in shape. The dorsal furrow is wide and relatively deep, as are the other furrows. The glabella, convex in both directions, stands completely above the librigenes. In cross section it has a sub-circular outline and longitudinally it is curved throughout, but has nearly all of its convexity in the anterior half. The brim is relatively wide and flat, with rather sharply depressed ends. The fixigenes are about one-third the width of the glabella and their anterior portions are about half of their average width. The eyes are long, extending forward almost the full length of the glabella.

Wilberns formation; (loc. 70) Baldy Mountain, 8 miles northwest of Burnet, Texas.

*Holotype*.—U.S.N.M. No. 108658a; paratypes, Nos. 108658b, c.

#### IRVINGELLA BACCA, new species

PLATE 3, FIGURES 34-36

This small, well-defined species is not as abundantly represented as the others found at the locality. The glabella contracts slightly to a rounded front. Occipital and rear glabellar furrows deeply impressed; anterior pair faint and the median pair well developed as shown in side view. The entire cranidium is convex longitudinally, the glabella having its greatest convexity in the anterior half, where it overhangs

the anterior furrow. In cross section it has a distinctly flattened outline, although it stands completely above the fixigenes. The brim is of normal width, slightly thickened, and because of the depressed anterior angles, appears to be sinuate when viewed from the front. Fixigenes, nearly half the width of the glabella, are convex and slope downward from the dorsal furrow at an angle less than the lateral slope of the glabella. They are also arched longitudinally and contract in the anterior portion to a small fraction of their average width. In dorsal view the anterior fixigenes appear narrow, owing to the nearly vertical position of their outer portions.

Wilberns formation; (loc. 14b) Cold Creek Canyon, opposite north end of Sponge Mountain, San Saba County, Texas.

*Holotype*.—U.S.N.M. No. 108659.

#### IRVINGELLA ACCINCTA, new species

PLATE 3, FIGURES 37-39

The glabella, clearly defined by a rather deep dorsal furrow, contracts rather strongly in the anterior portion to a rounded front. In the exfoliated holotype the occipital and two pairs of glabellar furrows are well developed, but the anterior pair seems to be lacking. In cross section the glabella is distinctly flattened, and longitudinally has most of its convexity in the anterior third. The brim is rather wide and at its ends considerably depressed. The anterior fixigenes first slope downward toward the front, then upward to meet the down-turned ends of the brim. The fixigenes at their widest point are about half the width of the glabella. They are convex laterally, rising considerably above the bottom of the dorsal furrow and then sloping down more gently, so that the eye is only slightly below the dorsal furrow. The eye band is prominent because of the deep palpebral furrow and the slight thickening of the band. The posterolateral limbs are also curved into a vertical position.

Wilberns formation; (loc. 14b) Cold Creek Canyon, opposite north end of Sponge Mountain, San Saba County, Texas.

*Holotype*.—U.S.N.M. No. 108660.

#### IRVINGELLA ABRUPTA, new species

PLATE 3, FIGURES 40-45

Like the other species at the locality, *I. abrupta* is about average size for the genus. It is represented by several cranidia. The glabella is prominent both for its large size and for its convexity, the species deriving its name from the latter feature which serves to distinguish

it from its associates. In the exfoliated holotype the occipital and the three glabellar furrows increase in depth toward the rear of the cranidium. The dorsal furrow is broad and on the outside of the test is indicated only by change of curvature. The glabella is constricted anteriorly by the circular course of the dorsal furrow. Laterally the glabella is highly arched, being only slightly flattened on top. Longitudinally it is very convex so that the front half slopes downward sharply from the horizontal line. The thick brim is sinuate in front view and is slightly up-turned with respect to the anterior furrow. Fixigenes nearly half the width of the glabella, narrowing rapidly forward from their midpoint, to one-fourth average width. Eyes moderately long extending from about the ends of the occipital furrow forward to the anterior angles of the dorsal furrow. In dorsal view the eyes curve only slightly for half their length from the occipital furrow, then more abruptly. Laterally the fixigenes are only slightly convex, except where they are rolled under at their outer edges, and as a whole assume a nearly horizontal position with respect to the base of the cranidium. Longitudinally they conform to the great convexity of the head, but more by means of sloping forward as a whole than by curving. In this respect *I. abrupta* is unique. Test smooth, but exfoliated specimens have the usual strongly punctate surface.

Wilberns formation; (loc. 14b) Cold Creek Canyon, opposite north end of Sponge Mountain, San Saba County, Texas.

*Holotype*.—U.S.N.M. No. 108661a; paratype, No. 108661b.

#### IRVINGELLA MEDIA, new species

##### PLATE 3. FIGURES 46-54

This relatively small, abundant species is wider than the other Texas species and in this respect finds closer relatives in the Canadian Rockies.

The glabella is long, narrow, and considerably constricted toward the front. The occipital furrow and rear glabellar furrows are wide and fairly deep, while the anterior pairs have normal development. Viewed vertically, this species seems to be very broad and flat. From the front it is broad even though the glabella is highly arched. Longitudinally, however, as the side views show, this species is strongly convex. The brim is rather wide and has a somewhat thickened edge and a shallow anterior furrow. The fixigenes at their widest are about half the width of the glabella at the same point. Their rear moiety is nearly rectangular in shape, but the anterior portion decreases rapidly in width, being reduced finally to the width of the

brim. The eyes are long, extending almost from the occipital furrow to a point beyond the anterior angle of the dorsal furrow. They first curve outward from their rear end for about a third of their length, then bend at a rather sharp angle toward the glabella.

Wilberns formation; (loc. 70) Baldy Mountain, 8 miles northwest of Burnet; and (loc. 14b) Cold Creek, opposite north end of Sponge Mountain, San Saba County, Texas.

*Holotype*.—U.S.N.M. No. 108662a; paratypes, Nos. 108662b, 108663.

**IRVINGELLA ALBERTA, new species**

PLATE 4, FIGURES 1-3

The wide glabella tapers more rapidly than the average for the genus. The occipital and first pair of glabellar furrows are very deep and wide. The middle pair consists of short, sharply impressed indentations at the sides of the glabella, and the anterior pair appears only as slight depressions. Laterally the glabella stands completely above the dorsal furrow, its outline being slightly flattened on top. Longitudinally it is curved throughout. The brim is evenly convex and of average width. The fixigenes are less than one-third the glabellar width anterior to the eyes, narrowing rapidly to match the rim width. Owing to the sharp depression of the anterior angles and the tapered glabella the entire cranium narrows perceptibly forward.

Lyell formation; (loc. 19u) Johnson Creek, 8 miles east of Lake Louise, Alberta.

*Holotype*.—U.S.N.M. No. 108664.

**IRVINGELLA RICHMONDENSIS, new species**

PLATE 4, FIGURES 4-6

This small species with a wide cranium has relatively the widest fixigenes of any Nevada species.

The glabella is subcylindrical, tapering slowly forward. The occipital and first pair of glabellar furrows are narrow and their position is more nearly parallel to the rear margin of the glabella than is usually the case. Laterally the glabella has a nearly semicircular outline. Longitudinally it is rather convex, increasing in convexity from the rear margin forward. The brim is relatively large and somewhat thickened, sloping down in line with the declivity of the head. Fixigenes more than half the width of the glabella, decreasing in their anterior portions to the width of the brim. Longitudinally they are

rather tumid in the rear moiety. Laterally they first rise from the broad dorsal furrow, then slope gradually to their outer margins.

Secret Canyon shale; (loc. 60) near Richmond Mine, Eureka District, Nevada.

*Holotype*.—U.S.N.M. No. 108665.

**IRVINGELLA ADAMSENSIS, new species**

PLATE 4, FIGURES 7-11

Like the other species at this locality, *I. adamsensis* has a relatively slender glabella and wide cranidium. It is represented by a number of cranidia.

The glabella is constricted toward the truncated front. The furrows are developed about as usual, but a peculiar feature is found in the slight depression in the sides of the ridge between the occipital and first glabellar furrows. In cross section the glabella has a flattened curvature, and longitudinally it curves with the cranidial convexity. The rather wide and thickened brim is striated in the middle. The fixigenes are about half the width of the glabella, a width they maintain with little change in the rear half, but in the anterior portion gradually contract to the width of the brim. Laterally the fixigenes are rather convex, rising from a fairly deep glabellar furrow.

Secret Canyon shale; (loc. 60) near Richmond Mine, Eureka District, Nevada.

*Holotype*.—U.S.N.M. No. 108666a; paratype, No. 108666b.

**IRVINGELLA FLOHRI, new species**

PLATE 4, FIGURES 12-14

This well-represented species is large compared to its associates.

The glabella tapers forward to a rather straight front margin, and the furrows are developed about as usual. Laterally the convexity of the glabella is greatly reduced, though longitudinally it curves at an even rate. The brim is of normal width, slightly rolled. The fixigenes are about half the width of the glabella in their rear half, while the anterior portion is very convex, overhanging the eyes at the anterior angles. The eyes are very long, and the eye band is conspicuously developed.

The specific name is given in recognition of Dr. M. C. Flohr, who was my assistant at the time when some of the fossils were collected.

Secret Canyon shale; (loc. 60) near Richmond Mine, Eureka District, Nevada.

*Holotype*.—U.S.N.M. No. 108667.



**IRVINGELLA TUMIFRONS** (Hall and Whitfield)

PLATE 4, FIGURES 42, 43

*Chariocephalus tumifrons* HALL and WHITFIELD, U. S. Geol. Expl. 40th Par., vol. 4, p. 224, pl. 2, figs. 38, 39, 1877.

*Irvingella tumifrons* RESSER, Smithsonian Misc. Coll., vol. 97, No. 10, p. 33, 1938.

*Irvingella (Irvingellina) tumifrons* KOBAYASHI, Jap. Journ. Geol. Geogr., vol. 15, Nos. 3-4, p. 175, 1938.

The present study has led to the conclusion that this species belongs in *Irvingella*. Several additional cranidia, distorted in other directions than in the holotype, allow a reconstruction. It will be observed in figure 43 that on the left side of the specimen, as mounted, an anterior furrow seems to separate a rim and preglabellar area, but on the other side none appears. From the fact that other specimens also fail to show an anterior furrow, we may conclude that this seeming furrow is merely the result of compression. It is, of course, possible that all species of both *Irvingella* and of *Chariocephalus*, if they have a fairly wide anterior angle, may possess an incipient anterior furrow.

Secret Canyon shale; Pogonip Mountain, White Pine District, Nevada.

*Holotype*.—U.S.N.M. No. 24561.

**PARAIRVINGELLA** Kobayashi, 1938

*Parairvingella* KOBAYASHI, Jap. Journ. Geol. Geogr., vol. 15, Nos. 3-4, p. 175, 1938.

Kobayashi erected *Parairvingella* as a subgenus, based on the Nevada specimen which Walcott erroneously identified as *Chariocephalus tumifrons* Hall and Whitfield, renaming it *Irvingella (Parairvingella) angustilimbatus*. Long ago I recognized the distinctness of this specimen, not only specifically, but generically, and so labeled it. Kobayashi extracted his data from my partially completed notes. Even though there is no striking difference between *Parairvingella* and related genera, there seems to be sufficient difference to raise it to full generic rank. I have referred *Irvingella arctica* Walcott and Resser from Novaya Zemlya to the same genus as Walcott's Nevada specimen, although some doubt of its true generic affinity still remains. At the same time three new species are recognized among the Nevada material.

*Parairvingella* has the glabellar and eye structure like *Irvingella*, and a brim consisting of a narrow preglabellar area and rim. The distinctive feature is the preglabellar area in which we find a transi-

tional structure between *Drumaspis* on the one hand and *Elvinia* on the other.

*Genotype*.—*Chariocephalus* (?) *tumifrons* Walcott (not Hall and Whitfield).

#### PARAIRVINGELLA ANGUSTILIMBATA Kobayashi

PLATE 4, FIGURES 18-22

*Chariocephalus tumifrons* WALCOTT (not Hall and Whitfield), U. S. Geol. Surv. Monogr. 8, p. 61, pl. 10, fig. 16, 1884.

*Irvingella* (*Parairvingella*) *angustilimbatus* KOBAYASHI, Jap. Journ. Geol. Geogr., vol. 15, Nos. 3-4, p. 175, 1938.

This species, represented by a number of crania, is recognized at several localities. It is characterized by a wide glabella with furrows of normal development. The glabella stands well above the fixigenes. In cross section it is very steep at the sides but is flattened on top. Longitudinally it has a marked convexity, most of which is in the anterior half. The narrow brim consists of a clearly defined thickened rim and a narrower preglabellar area. The slightly convex fixigenes are almost exactly half the width of the glabella, and slope down from the dorsal furrow. Posterolateral limbs depressed to a vertical position. Anterior fixigenes also sharply depressed. The eyes are long, extending forward almost to the anterior furrow, and are angulated at about the midpoint.

Secret Canyon shale; (locs. 62, 63) north of Adams Hill, Eureka District, Nevada.

*Holotype and paratypes*.—U.S.N.M. No. 24643; plesiotypes, No. 108672.

#### PARAIRVINGELLA EUREKENSIS, new species

PLATE 4, FIGURES 15-17

The narrow glabella tapers a little in the anterior third to a rounded front. The occipital and first pair of glabellar furrows are wide and deep, and in the exfoliated holotype the other two pairs are visible. Laterally the glabella is arched above the dorsal furrow. Longitudinally it also has considerable convexity, most of which is attained in the anterior fourth. The fixigenes are slightly more than half the width of the glabella and, since the eyes are not greatly bowed, maintain their maximum width in the posterior two-thirds. Anteriorly the fixigenes contract to about half their greatest width, and are considerably depressed. The eyes are moderately long, and, because of the wide anterior fixigenes, do not reach the line of the dorsal furrow.

Brim rather wide, with a thickened, slightly upturned rim and a preglabellar area of about equal width. Viewed laterally the preglabellar area appears to be merely an extraordinarily wide anterior furrow. That this is not the case is shown in the anterior fixigenes, on which the anterior furrow is clearly seen in normal position.

Secret Canyon shale; (loc. 61) south of the Hamburg Mine, Eureka District, Nevada.

*Holotype*.—U.S.N.M. No. 108668.

**PARAIRVINGELLA INTERMEDIA**, new species

PLATE 4, FIGURES 25-31

This is the most common species in the Eureka District. It is characterized by great width, comparable to typical *Irvingella*. The glabella is wide and has a circular outline in front, with the usual furrows clearly defined. It stands completely above the shallow dorsal furrow, and longitudinally attains its convexity in the anterior third. The fixigenes are about half the width of the glabella, contracting in their anterior portions to about half their average width. The long eyes attain their moderate curvature by a sharp bend near their midpoint. The brim is narrow and consists of a thickened upturned rim and a narrow preglabellar area of equal width. The posterolateral limbs are bent down very sharply, while the anterior fixigenes decline into the anterior angles to a lesser degree.

Secret Canyon shale; (loc. 61) south of Hamburg Mine, Eureka District, Nevada.

*Holotype and paratypes*.—U.S.N.M. No. 27018.

**PARAIRVINGELLA HAMBURGENSIS**, new species

PLATE 4, FIGURES 23, 24

Development of a wide, vertically striated preglabellar area gives this species somewhat the appearance of *Elvinia*, but for the present it may remain in *Parairvingella*.

The subconical glabella shows the usual furrows. Although not highly convex in cross section it rises above the fixigenes. Longitudinally the rear portion is little curved, but the anterior third curves sharply downward. The brim width is nearly equal to one-fourth the cranidial length and consists of a thickened upturned rim and a preglabellar area of about equal width. The fixigenes average less than half the glabellar width and maintain their width except in the anterior portion where there is a reduction of about a third. The test is granulated and the preglabellar area marked by vertical lines.

Secret Canyon shale; (loc. 61) south of Hamburg Mine, Eureka District, Nevada.

*Holotype*.—U.S.N.M. No. 108669.

**DRUMASPIS, new genus**

This beautiful trilobite, represented by numerous species, carries development of the *Chariocephalus-Irvingella* line in a logical direction toward more normal trilobite structure by reducing eye size and enlarging the posterolateral limbs. The brim always has a narrow preglabellar area, but taken as a whole, the departure from the bar structure, characteristic of the other komaspid genera, is not great.

The quadrangular glabella is more or less tapered and usually has rounded anterior angles. Occipital furrow deep. Three pairs of glabellar furrows normally developed, the rear pair generally, and the second pair sometimes, connected across the middle. Dorsal furrow deep throughout. Fixigenes confined very largely to palpebral lobes and posterolateral limbs. Eyes large, varying from less than half to more than two-thirds the cranidial length; usually set at an angle to the cranidial axis. Eye bands wide. Brim narrow, of even width, and its length equals the width of the rear portion of the glabella. Thickened rim about as wide as preglabellar area. Anterior fixigenes narrow. Anterior facial suture usually vertical, but sometimes divergent. Posterolateral limbs fairly large in the smaller-eyed species.

Libragenes small, with thickened rim. Ocular platforms narrow in front, increasing in width posteriorly.

Pygidium not found. Surface usually granulose.

*Genotype*.—*D. walcotti*, new species.

**DRUMASPIS WALCOTTI, new species**

PLATE 4, FIGURES 37-41

This species has a long glabella which tapers slightly. Three pairs of glabellar furrows are clearly discernible. The fixigenes vary considerably in width owing to the strong curvature of the eyes. At their widest point they are a little more than a third of the glabellar width. The brim consists of a thickened rim and a slightly narrower preglabellar area. The glabella is slightly arched in cross section, and longitudinally curves considerably more, particularly in the anterior portion. The conspicuously wide eye bands at once set the species off from others found in the vicinity.

St. Charles formation; (locs. 4y, 5e) Two Mile Canyon, Wasatch Mountains, Idaho.

*Holotype*.—U.S.N.M. No. 108670a; paratype, No. 108670b.

**DRUMASPIS IDAHOENSIS, new species**

PLATE 4, FIGURES 32-36

This species is represented by many cranidia. The glabella tapers slightly. Peculiar structure is shown by the occipital furrow, which is narrow next to the dorsal furrow, then widens suddenly, maintaining that width to the similar point on the opposite side. The rear pair of glabellar furrows is interrupted in the middle both by growing shallow and by making a reversed forward curve. The anterior pairs show on exfoliated specimens. In cross section the glabella is rather flat but stands completely above the dorsal furrow. In longitudinal section it curves gently for most of its length, then turns down sharply at the front. The narrow brim consists of a rim in horizontal position. The fixigenes are a little less than one-third the glabellar width and in their anterior portion decrease to about the width of the anterior dorsal furrow. They slope downward rather evenly from the dorsal furrow, their declivity increasing in the rear to meet the sharply depressed posterolateral limbs, and anteriorly to join the rim. The moderately bowed eyes attain a length equal to about half the length of the glabella.

St. Charles limestone; (loc. 4y) Two Mile Canyon, 2 miles south of Malad, Wasatch Mountains, Idaho.

*Holotype*.—U.S.N.M. No. 108671a; paratype, No. 108671b.

**DRUMASPIS ALBERTA, new species**

PLATE 5, FIGURES 1-3

The description of this species is based on several cranidia, the most complete example being figured as the holotype.

The quadrangular glabella has a slightly indented anterior margin. Anterior angles rounded. In cross section the glabella is only slightly arched above the dorsal furrow. Longitudinally there is considerable elevation, most of which occurs in the anterior fourth. Brim narrow, apparently with a narrow upturned rim. Fixigenes about half the width of the glabella; anterior portion reduced to brim width. Eyes not strongly bowed, set at a wide angle to the dorsal furrow, forming a fixigene of fairly even width for the rear two-thirds of the head.



The fixigenes are almost flat and slope down from the dorsal furrow in line with the lateral slope of the glabella. Surface finely granulose.

Lyell formation; (loc. 64x) Ranger Brook Canyon, Sawback Range, Alberta.

*Holotype*.—U.S.N.M. No. 108673.

**DRUMASPIS BRISCOENSIS, new species**

PLATE 5, FIGURES 4-8

This species is represented by several cranidia, of which two exfoliated examples are figured.

The glabella is rectangular, with a practically straight front margin and slightly rounded anterior angles. Four sets of furrows are clearly defined in exfoliated specimens. In cross section the glabella rises with a flat curvature above the dorsal furrow, while longitudinally it is curved throughout, the curvature increasing from the rear forward. Brim of moderate width consists of a thickened rim, widened slightly in the middle. Fixigenes at their widest point slightly more than a fourth the glabellar width. Eyes rather sharply bowed. Anterior fixigenes depressed sharply. Portion of the test preserved appears to be smooth.

Sabine formation; (loc. 17p) Radium Hot Springs, Brisco Range, British Columbia.

*Holotype*.—U.S.N.M. No. 108674a; paratype No. 108674b.

**DRUMASPIS GOODSIRENSIS, new species**

PLATE 5, FIGURE 9

Only the holotype cranidium has been found at this locality.

The glabella tapers slightly forward to a straight anterior margin. The usual three pairs of glabellar furrows are developed. Owing to crushing in the shale matrix, the convexity cannot be determined. The fixigenes at their widest point are a little more than a third the glabellar width. The eyes are not greatly bowed and, because of the relatively great width of the anterior fixigenes, depart from the course of the dorsal furrow only at a small angle. Brim of average width, consisting of a slightly thickened rim of about the same width as the anterior furrow.

"Goodsir" formation; Moose Creek, Ottertail Range, British Columbia.

*Holotype*.—U.S.N.M. No. 108675.

**DRUMASPIS SABINENSIS**, new species

PLATE 5, FIGURES 10, 11

This distinctive species is represented only by a few cranidia.

The rectangular glabella is rather long and rounded at the anterior angles. Both laterally and longitudinally it has average convexity for the genus. The moderately wide brim is made up about equally of anterior furrow and rim. The rim has a horizontal position and widens out in the middle. The fixigenes, at their widest point, are less than one-third the glabellar width. Their anterior portions are turned down sharply, leaving a small ridge which extends into the preglabellar area. The eyes are of moderate size and moderately bowed.

Sabine formation; (loc. 17s) Sabine Mountain, 2 miles northeast of Canal Flats, Brisco Range, British Columbia.

*Holotype*.—U.S.N.M. No. 108676.

**DRUMASPIS MAXWELLI**, new species

PLATE 5, FIGURES 12, 13

About a dozen cranidia of this species are available.

The glabella is of normal shape and proportion, rounded at the anterior corners. The usual glabellar furrows are present but not deeply impressed. In cross section the glabella stands completely above the fixigenes and dorsal furrow, rising steeply on the sides, but is flattened on top. Longitudinally the cranidium is considerably arched, the convexity increasing from the rear forward. The brim is of normal width and upturned to a slightly thickened brim, which in the holotype cranidium is partly broken off. Fixigenes are narrow, being little more than one-fourth the glabellar width. Their anterior portion is about as wide as the brim and is turned down at the anterior angles. The eyes are of moderate size and slope outward at a small angle.

St. Charles limestone; (loc. 66z) St. Charles Canyon, Bear River Range, Idaho.

*Holotype*.—U.S.N.M. No. 108677.

**DRUMASPIS DECKERI**, new species

PLATE 5, FIGURES 14-16

Even though the available material is confined to the illustrated holotype, the species is so distinctive that it merits description. The quadrangular glabella is rounded at the anterior angles and slightly indented in front. Glabellar furrows developed as usual, the rear

pair containing pits on each side of the medial line. Laterally the glabella is only moderately convex, but longitudinally it is considerably more curved. The brim is of normal width, consisting mainly of a wide rim, in horizontal position, with a lingual extension in the middle. The fixigenes at their widest point are a little less than one-third the glabellar width, and their anterior portions, being sharply depressed, are narrower than the brim. The large eyes are sharply bowed.

Honey Creek limestone; (loc. 91b) 4 miles southeast of Hennepin, West Timbered Hills, Arbuckle Mountains, Oklahoma.

*Holotype*.—U.S.N.M. No. 108678.

**DRUMASPIS OSELLA, new species**

PLATE 5, FIGURES 17-20

Among the numerous specimens of the genus in the Texas collections, two cranidia present very distinct characteristics and are thus separated from *D. texana*. The glabella tapers forward more than the average amount for the genus and is rounded at the anterior angles to a straight front margin. Four pairs of glabellar furrows are defined. In cross section the entire cranidium is convex, the glabella standing above the dorsal furrow with a rather flat curvature. Longitudinally the head is rather convex, the greatest amount being in the anterior third. Brim rather wide, consisting of a thickened rim and a slightly narrower preglabellar area. The fixigenes at their widest point are less than one-third the width of the glabella. Their anterior portion is slightly wider than the preglabellar area. The eyes are evidently sharply bowed and not very large. Both the anterior angles and the posterolateral limbs are depressed rather sharply. The surface, except in the furrows, is ornamented with anastomosing lines, which, in places, practically form granules.

Wilberns formation; (loc. 70) Baldy Mountain, 8 miles northwest of Burnet, Texas.

*Holotype*.—U.S.N.M. No. 108679a; paratypes Nos. 108679b, c.

**DRUMASPIS TEXANA, new species**

PLATE 5, FIGURES 27-30

This species is represented by numerous specimens from several localities. The rather wide glabella contracts slightly forward and is well rounded at the anterior angles. The rear pair of glabellar furrows is deeply impressed, the next pair faint, and the forward pair very faint. In cross section the glabella is elevated as usual, longitudinally it is curved throughout. The brim consists of a narrow preglabellar

area and a slightly thickened rim expanding in the middle. Fixigenes at their widest point are a little less than one-third the glabellar width. Eyes of moderate size, rather sharply bowed. Anterior fixigenes about as wide as the brim, increasing forward into the down-turned anterior angles. Surface granulated.

Wilberns formation; (loc. 70) Baldy Mountain, 8 miles northwest of Burnet, Texas; and (loc. 670) Potatotop, 7 miles northwest of Burnet, Texas.

*Holotype*.—U.S.N.M. No. 108684a; paratype Nos. 108684b, c.

#### DRUMASPIS WICHITAENSIS, new species

PLATE 5, FIGURES 21, 22

More than 10 cranidia of this species are in the collection. The quadrate glabella is rounded by even curves at the anterior angles. Glabellar furrows are developed normally except that the front pair is almost obsolescent. In cross section the glabella stands completely above the fixigenes, rising rather steeply at the sides and flattened on top. Longitudinally the cranidium is high, with the front lobe of the glabella standing vertical. Brim of moderate width, consisting of a narrow preglabellar area and a slightly widened rim in horizontal position. Fixigenes narrow, at their widest point being a little more than one-fourth the width of the glabella. Anterior fixigenes sharply down-curved, attaining a width at the anterior angles of slightly more than the brim. Eyes rather small and highly bowed, with practically a circular course. Posterolateral limbs curved downward into a vertical position. Surface faintly marked by anastomosing lines.

Honey Creek limestone; (loc. 91u) 1 mile east of Canyon Creek, 15 miles northwest of Fort Sill, Wichita Mountains, Oklahoma.

*Holotype*.—U.S.N.M. No. 108680.

#### DRUMASPIS CLARA, new species

PLATE 5, FIGURES 23-26

Several cranidia and a librigena represent this species.

The glabella tapers forward to a nearly circular frontal outline. Glabellar furrows developed normally. In cross section this is a highly convex species. The glabella, standing completely above the librigenes, rises with a rather even curvature throughout. Longitudinally the cranidium also has high relief, likewise attained by a rather even curvature. Brim is of normal width. The slightly thickened rim widens in the middle, and occurs in a horizontal position. Fixigenes slightly less than one-third the glabellar width, their anterior portion

rather wide and depressed at the anterior angles. The eyes are of moderate size and not greatly bowed. The associated librigena has a heavy, striated rim, so constructed that it shows the suture to be intermarginal for more than one-third the width of the head. Ocular platform rather small, and covered with anastomosing lines similar to the elevated portions of the cranium.

Honey Creek limestone; (loc. 91s) West Timbered Hills, Arbuckle Mountains, Oklahoma.

*Holotype*.—U.S.N.M. No. 108681a; paratype No. 108681b.

**DRUMASPIS NITIDA, new species**

PLATE 5, FIGURES 34, 35

This species is represented by several crania. The wide, nearly quadrate glabella is well rounded in front. All the furrows are moderately developed. The brim is normal in width and consists of a narrow preglabellar area, and a slightly thickened rim which broadens toward the middle. The fixigenae are narrow, at their widest point being little more than one-fourth the glabellar width. In their anterior portions they are about the same width as the brim, but widen toward the depressed anterior angles. The eyes are somewhat larger than average size and slightly bowed, the bowing attained by a sharp angular turn near the midpoint. A distinctive feature is the extraordinary width of the eye band. Surface covered by irregular raised lines which are equivalent to irregular curved granules.

Honey Creek limestone; (loc. 91s) West Timbered Hills, Arbuckle Mountains, Oklahoma.

*Holotype*.—U.S.N.M. No. 108682.

**DRUMASPIS UTAHENSIS, new species**

PLATE 5, FIGURES 31-33

In the National Museum collections are several crania which when first studied were thought to belong to *Chariocephalus*. However, when comparison was made with typical forms of that genus and of *Drumaspis*, they appeared to be nearer the latter.

The quadrangular glabella has a straight anterior margin and rounded anterior angles. The glabellar furrows are well developed, and even the anterior pair may be traced across the glabella. In cross section the glabella stands completely, but not high, above the dorsal furrow and is nearly flat on top. Longitudinally the relief is considerable, but the curvature is nowhere great except in the very front of the cranium. The fixigenae are wide, being half the glabellar



width at their widest point. The very long eyes are curved so sharply that the two halves are almost at right angles to each other. Anterior fixigenes practically wanting and on the whole are nearly flat, sloping down from the dorsal furrow. The posterolateral limbs are very sharply depressed.

St. Charles limestone; (loc. 54x) Two Mile Canyon, 2 miles south of Malad, Wasatch Mountains, Idaho.

*Holotype*.—U.S.N.M. No. 108683.

#### UNCLASSIFIED GENERA

##### CHEILOCEPHALUS Berkey, 1898

##### CHEILOCEPHALUS WICHITAENSIS, new species

##### PLATE 5, FIGURE 39

Several cranidia of this interesting genus have been found in the Oklahoma collections. It is a very simple trilobite, the cranidium consisting of a large glabella with no furrows except a shallow occipital furrow. The fixigenes are simple. The glabella tapers slightly to a nearly straight anterior margin. In cross section it stands well above the dorsal furrow, rising at a fairly even rate to approximately the center. Longitudinally, the head has considerable relief, attained by even curvature. The brim is narrow and consists of a simple, slightly concave, and nearly horizontal extension, the outer edge of which is very slightly thickened but does not form a rim. The fixigenes have nearly the same width throughout, and are about equal to one-fourth the glabellar width. Test smooth.

Compared to *C. strobilensis* the Oklahoma species is slightly smaller and differs in the distribution of convexity in both directions.

Honey Creek limestone; (loc. 9p) 15 miles northwest of Fort Sill, Wichita Mountains, Oklahoma.

*Holotype*.—U.S.N.M. No. 108685.

##### CHEILOCEPHALUS TEXANUS, new species

##### PLATE 5, FIGURES 36-38

The one small cranidium in the Texas collections has a smooth rectangular glabella, rounded in front. In cross section it forms a continuous curve with the fixigenes, which are barely separated by the dorsal furrow. Longitudinally, the cranidium is convex, with a rather even curvature, increasing in the anterior portion. The brim, on the whole, is slightly concave. No anterior furrow is developed, but a thickened rim turns up slightly, and is thereby separated from

the preglabellar area. The fixigenes, at the rear of the eyes, are about half the glabellar width and form wide triangular posterolateral limbs. Anterior to the rather small eye they are somewhat wider than the brim. As the cranium has no occipital furrow, it presents a very smooth appearance.

Hickory sandstone; (loc. 68z) Packsaddle Mountain, 11 miles southeast of Llano, Texas.

*Holotype*.—U.S.N.M. No. 108686.

#### CHEILOCEPHALUS BUTTSI, new species

##### PLATE II, FIGURE 6

Unfortunately many years ago the holotype and other cranidia representing the species were damaged by poor preparation. This cranium is fully typical of the genus, even as to size. The large glabella extends the full length of the head and has three pairs of shallow furrows. It tapers only slightly. Though incomplete the fixigenes are seen to be small anterior to the large posterolateral limbs. Longitudinally the cranium is little curved except in the anterior fourth where the slope becomes vertical. In cross section the entire head has considerable convexity attained by a rather evenly convex glabella and continued by the lateral slopes of the fixigenes.

Surface beautifully shagreened.

Ore Hill limestone; (loc. 107v)  $\frac{1}{2}$  mile northwest of Drab, Pennsylvania.

*Holotype*.—U.S.N.M. No. 108746.

#### CHOLOPILUS Raymond, 1924

#### CHOLOPILUS NEVADENSIS, new species

##### PLATE 6, FIGURES 1-2

The main features of this species relate it to *Cholopilus*. Furthermore its stratigraphic position is approximately the same as other representatives of the genus. Numerous cranidia are in hand, but no other parts.

*C. nevadensis* is characterized by its simplicity. The very large, smooth glabella extends nearly to the anterior margin. The dorsal furrow, fairly well impressed in the rear, decreases in depth forward until beyond the eye it can be observed only as a very faint line beneath the surface. A weak occipital furrow is developed but no glabellar furrows show on the outer surface. Exfoliated specimens have the merest trace of three pairs of glabellar furrows, the first pair recurved, the second pair turning a bit forward, and the third again

turned backward, so that the second and third pairs form a faint cross on the glabella. Laterally the glabella is rather evenly but flatly arched; longitudinally it is considerably curved. The brim continues the rounded curvature of the glabella and consists of a preglabellar area and a narrow, wirelike rim, but faintly indicated. Fixigenes at their widest point are about one-fifth of the glabellar width, and they maintain practically the same width throughout. The eyes are of normal size, situated about the midpoint of the cranidium. A faint tubercle which has more the appearance of a median eye than of a spine occurs on the occipital ring.

Hamburg limestone; (loc. 23d) near Hamburg Mine, Eureka District, Nevada.

*Holotype*.—U.S.N.M. No. 108687.

### CHOLOPILUS (?) ALBERTENSIS, new species

#### PLATE 10, FIGURE 3

This cranidium of doubtful generic position is described in order to present the faunal element. Because there are no good illustrations of the type of *Cholopilus* extant, one cannot be sure that the published drawings rightly portray the glabellar proportions. The general appearance of this trilobite places it nearest to *Cholopilus*, in which genus it may be placed for the present.

The glabella is wide, occupying more than half the cranidial area. It is defined by a dorsal furrow so faint that it disappears in certain light. This cranidium is convex in both directions, the curvature being greater longitudinally than laterally. The anterior margin is slightly indented in the middle and a very faint rim is indicated.

Lyell formation; (loc. 64b) Glacier Lake Canyon Valley, 48 miles northwest of Lake Louise, Alberta.

*Holotype*.—U.S.N.M. No. 108733.

### CALYPTOMMA, new genus

A small trilobite characterized by simplicity of structure. The large glabella is quadrate except for constriction at the anterior angles. Glabellar furrows are very faint even on exfoliated specimens. Brim a simple bar. Fixigenes very small, confined to the palpebral lobe, and in the genotype are less than half the width of the eye band. Eyes so large that they envelop the glabella, extend from the forward margin of the glabella beyond the occipital ring. Eye band wide.

This genus resembles *Cholopilus* Raymond in the simplicity and arrangement of the various cranidial parts. It differs from that genus

in two respects: first, the fixigenes are narrower, and second, the eyes are very much larger.

Surface marked by elongate granules on the elevated portions.

Name.—*καλυπτω* = envelop; *ὄμμα* = eye.

*Genotype*.—*C. typicale*, new species.

**CALYPTOMMA TYPICALE**, new species

PLATE 12, FIGURES 8, 9

The generic description and illustrations present the specific characters.

Red Lion formation; (loc. 150e) Boulder Creek, 1 mile north of Princeton, Montana.

*Holotype*.—U.S.N.M. No. 108753a; paratype, No. 108753b.

**ILLAENURUS** Hall, 1863

**ILLAENURUS PRISCUS**, new species

PLATE 6, FIGURES 3-7

This species, though not fully typical of *Illaenurus*, does not seem to warrant the establishment of a separate genus. The four cranidia figured differ slightly in proportions, and therefore it is possible that two species are included. Departure from essential features of *Illaenurus* is found in the great width and faint delimitation of the glabella. Exfoliated specimens show a completely outlined glabella, and a considerable width of fixigene. It has generally been assumed that *Illaenurus* has no fixigenes, or in other words, that the dorsal furrow passes through the two ends of the eye lobe.

In general outline the cranidium is nearly quadrate. *I. priscus* has a narrow, wirelike rim, and eyes of moderate size situated about the midpoint of the cranidium. Anterior to the eye the facial suture diverges slightly, and the anterior angles are turned down somewhat by a continuation of the cranidial slope. In cross section the glabella has a flat curvature, but longitudinally a much greater one.

Lyell formation; (locs. 66j, k) Ranger Canyon, Sawback Range, Alberta.

*Holotype*.—U.S.N.M. No. 108688a; paratypes Nos. 108688b, 108689a, b.

**ILLAENURUS ALBERTENSIS**, new species

PLATE 6, FIGURES 8-12; PLATE 14, FIGURE 18

This species is represented by numerous cranidia, and by a pygidium and librigena. It is not greatly unlike several undescribed species

from the Upper Mississippi Valley. On exfoliated cranidia the dorsal furrows show faintly for a short distance anterior to the eye, touching both ends of the eye lobe. Exfoliated specimens have a median eye situated about one-third the distance forward from the rear margin. In front of the eyes, which are situated behind the middle of the cranidium, the facial suture diverges considerably to form wide anterior angles. The thickened, heavily striated rim is almost vertical to the horizontal plane of the cranidium. In cross section the cranidium has a slight even curvature, but longitudinally it has considerably more relief, also attained by even curvature.

The librigenae forms nearly a quarter circle, with its convexity similar to that of the cranidium. The heavily striated border continues around the margin, decreasing toward the genal angle, which evidently bore no spine.

The pygidium is short, very wide, and lacks differentiation of axis or pleura. At the anterior margin two slight depressions indicate the presence of a very wide axis. The pygidium evidently came to rather sharp points at its lateral angles.

Portions of six simple thoracic segments remain articulated on one rock fragment.

Lyell formation; (loc. 20d) Tilted Mountain Brook, 9 miles east of Lake Louise, Alberta.

*Holotype*.—U.S.N.M. No. 108690a; paratype, No. 108690b.

**ILLAENURUS (?) SINCLAIRENSIS, new species**

PLATE 6, FIGURES 13-15

This species, doubtfully referred to *Illacnurus*, comes from somewhat older beds than those that contain the more characteristic species. The cranidium is wider than long and exclusive of the posterolateral limbs is rectangular in outline. No trace of dorsal furrows has been observed. In cross section this species is rather flat, but longitudinally it is considerably convex, with the anterior margin of the cranidium turned under. A peculiar feature is the development of a rim like that of *Platycolpus*. A small occipital tubercle suggests the presence of a medial eye, and short shallow multiple furrows near it evidently represent the occipital furrow. The eyes are of moderate size, situated slightly forward of the median point of the cranidium.

Sabine formation; (loc. 16t) Sinclair Canyon, Brisco Range, British Columbia.

*Holotype*.—U.S.N.M. No. 108691a; paratypes, Nos. 108691b, c.



**ILLAENURUS ELONGATUS (Walcott)**

PLATE 6, FIGURES 18, 19

*Tsinania elongata* WALCOTT, Smithsonian Misc. Coll., vol. 64, No. 3, p. 228, pl. 36, figs. 10, 10a, 1916.

The cranium on which this species is based is not average for *Illacnurus*. It is long and narrow, with little curvature in cross section but with somewhat more in longitudinal section. No dorsal furrow or rim seems to be differentiated. The anterior angles are rounded more than average for the genus. The eyes are about normal size, situated slightly forward of the glabellar midpoint.

McKay group; (loc. 23z) 2 miles west of Donald, Dogtooth Mountains, British Columbia.

*Holotype*.—U.S.N.M. No. 61736.

**PLATYCOLPUS Raymond, 1913****PLATYCOLPUS QUINNENSIS, new species**

PLATE 6, FIGURES 16, 17

The small collection from this locality has yielded a good cranium of *Platycolpus*, which is described because of its significance in the fauna. It is normal in all essential characters of the genus. A wide glabella, faintly indicated by a shallow dorsal furrow, extends a little in front of the eyes. The rim is wide and heavily striated. Anterior to the eyes the facial suture diverges, forming large anterior angles. The eyes are of moderate size, situated well back on the head. A shallow occipital furrow delimits a wide flat occipital ring.

Mendha limestone; (loc. 7j) Quinn Canyon Range, Nevada.

*Holotype*.—U.S.N.M. No. 108692.

**PLATYCOLPUS OKLAHOMENSIS, new species**

PLATE 6, FIGURES 20-25

This species is recognized at several localities. As usual only fragments of the cranium are preserved, a condition characterizing most species thus far recognized in the genus. The portion of the glabella available shows that it is wide, and rather evenly but not highly arched in both directions. It has the usual wide brim, although it lacks the usual striations.

The pygidium is normal in every respect. Exfoliated specimens show a well-separated axis. On the outer surface it is marked simply

by a change in slope. The pygidium is flatly convex in transverse section, but as may be observed from the illustration is much steeper in the opposite direction. The species is of average size and the surface seems to have been smooth.

Signal Mountain formation; (loc. 186s) 4 miles northwest of Ravia; (loc. 201j) Royer Ranch, Honey Creek, Arbuckle Mountains, Oklahoma.

*Holotype*.—U.S.N.M. No. 108693; paratypes, Nos. 108694a, b.

**PLATYCOLPUS WICHITAENSIS, new species**

PLATE 6, FIGURES 26-29

This species is represented by several cranidia and a pygidium, and even by a fragment of a librigena. *P. wichitaensis* averages slightly smaller than *P. oklahomensis*. The fragmentary cranidium figured has a faint dorsal furrow behind the eyes, and in both lateral and longitudinal sections is evenly and considerably arched. The eyes are of normal size and are situated about the midpoint of the cranidium. The brim is sharply demarcated, thickened, and heavily striated.

The pygidium on the same piece of rock with a cranidium of *Eureka*, is also highly arched in both directions and shows faint dorsal and axial furrows.

Signal Mountain formation; (loc. 12g) 2 miles southwest of Signal Mountain, Wichita Mountains, Oklahoma.

*Holotype*.—U.S.N.M. No. 108695a; paratype, No. 108695b.

**PLATYCOLPUS HIGHLANDENSIS, new species**

PLATE 6, FIGURES 30, 31

This species constitutes another important element of the fauna from the upper beds in the Highland Range, and consequently is described, even though the material is fragmentary. As usual no cranidia are preserved. The pygidium on which this species is based is itself incomplete, but has the normal generic features, and it is of rather large size. As shown in the illustrations the axis is faintly defined, tapering less rapidly than in other species. It is not highly arched in either direction, but has normal distribution of convexity.

Mendha limestone; (loc. 88) 7 miles north of Bennett Springs, Highland Range, Nevada.

*Holotype*.—U.S.N.M. No. 27017.

## PLATYCOLPUS SINCLAIRENSIS, new species

PLATE 6, FIGURES 32-36

Though there are in hand about 10 pygidia and about an equal number of librigenes, only one fragmentary cranidium, not altogether typical, has been found in the collection.

The librigena is almost flat in its rear portion but increases greatly in convexity forward, indicating that the cranidium must have been considerably arched longitudinally. The ocular platform is approximately a quarter circle and is surrounded by a wide, thickened, heavily striated border, with the striations turning toward the margin as the genal angle is approached.

The pygidium is rather convex, with the axis standing well above the pleural lobes, but the dorsal furrow is merely a change in slope. Several pleural furrows are visible on exfoliated specimens. The axis is rather long, extending beyond the midpoint of the pygidium.

Sabine formation; (loc. 16t) Sinclair Canyon, Brisco Range, British Columbia.

*Holotype*.—U.S.N.M. No. 108697a; paratypes Nos. 108697b, c.

## ENONTIOURA, new genus

Although up to the present time only the holotype pygidium has been discovered, it is given a new generic name because it represents such a strange form. On the same piece of rock is a rounded cranidium similar to that of *Camaraspis* but it is not well enough preserved to warrant description.

The specimen assumed to be a pygidium is characterized by a very large axis, which occupies most of its area. At the front of the wide axis is a half segment which looks more like a rim than the usual segmental division. Shallow dorsal furrows separate narrow pleural lobes, the dorsal furrow continuing very faintly around the rear of the axis. Beginning at the anterior angles a thickened, slightly upturned rim borders the outer edge of the pygidium. Aside from the peculiarity of shape and convexity, a very unusual feature is found in the striations which transverse the entire specimen from side to side, crossing both the axis and the pleural lobes. It is this feature which has several times raised the question as to whether this specimen is actually a trilobite pygidium or some oddly formed hypostoma, or even an undescribed crustacean. In view of these conditions, a description of this specimen is presented primarily to call it to the attention of geologists with the hope that its real position may be discovered.

Name.—*ενοντιος* = contrary; *ουρα* = tail.

*Genotype*.—*E. typicalis*, new species.

**ENONTIOURA TYPICALIS**, new species

PLATE 6, FIGURES 37, 38

The generic description, together with the illustrations, presents the characteristics of this peculiar form.

Mendha limestone; (loc. 88) 7 miles north of Bennett Springs, Highland Range, Nevada.

*Holotype*.—U.S.N.M. No. 108696.

**MACELLOURA** Resser, 1935**MACELLOURA TRANSVERSA**, new species

PLATE 7, FIGURE 1

When first observed this pygidium was thought to represent *M. dia*. Comparison shows that, while typical of the genus in every respect, the pygidium is wider than that of *M. dia*.

Wilberns formation; (loc. 14f) Bartlett Hollow, Burnet County, Texas.

*Holotype*.—U.S.N.M. No. 108698.

**ARAPAHOIA** Miller, 1936

*Arapahoia* MILLER, Journ. Pal., vol. 10, No. 1, p. 24, 1936.

*Hesperaspis* STOYANOW, Bull. Geol. Soc. Amer., vol. 47, No. 4, p. 469, 1936.

At the time *Arapahoia* was originally described, only the cranidium was known to the author. Specimens from the eastern front of the Beartooth Mountains identified with the genotype *A. typa* now add the librigenae and pygidium.

In the original description Miller pointed out the relationship of *Arapahoia* to *Plethometopus*, which occurs in younger Upper Cambrian strata. From the present study it becomes clear that *Norwoodella* described later is also related and that *Arapahoia*, *Norwoodella*, and *Plethometopus* form a single line of development. Thus far *Arapahoia* seems to be confined to horizons in the lower part of the *Cedaria* zone, and is the oldest genus of this group.

In spite of the abundance of examples, it is difficult to free good specimens of *Arapahoia*, because the matrix is refractory.

Exfoliated cranidia have well-defined dorsal and occipital furrows, and some species have three pairs of short glabellar furrows. A node on the base of the occipital spine may possibly be a median eye.

The librigenae is of moderate size. In some specimens a border is faintly indicated, but it scarcely breaks the even curvature as the ocular platform slopes to the margin. The entire librigenae extends into a longer or shorter genal spine.

The pygidium is short and wide, with a large axis, which seems to be segmented in all species. Some species have well-developed pleural furrows, and a few show a border.

#### ARAPAHOIA TYPA Miller

PLATE 7, FIGURES 37, 38

*Arapahoa typa* MILLER, Journ. Pal., vol. 10, No. 1, p. 25, pl. 8, fig. 6, 1936.

The figured specimens from the Beartooth Mountains are identified with the type species. However, without the holotype at hand for comparison, this identification is not without question.

Maurice formation; Butte north of Little Rocky Creek, Beartooth Mountains, Wyoming.

*Holotype*.—Columbia Univ. No. 12612; plesiotypes, U.S.N.M. No. 108708.

#### ARAPAHOIA STANTONI, new species

PLATE 7, FIGURES 2-4

This species is similar to *A. spatulata* Miller in that the glabella is not separated by relief from the fixigenes. The very shallow dorsal furrow can be seen very clearly in cross light. The keel shows in about the same degree as the glabella. Exclusive of the neck spine, the holotype canidium, measured immediately in front of the eyes, is 13.7 mm. long and 8.8 mm. wide. The anterior margin of the brim is slightly angulated. Few specimens retain the slender neck spine. The associated pygidium has two pleural furrows clearly defined.

Pilgrim formation; (loc. 26b) Mill Creek, Little Rocky Mountains, Montana.

*Holotype*.—U.S.N.M. No. 108699a; paratype, No. 108699b.

#### ARAPAHOIA REESIDEI, new species

PLATE 7, FIGURES 5-9

This species is represented by many specimens, but only a few can be cleaned reasonably well. *A. reesidei*, named for the collector, Dr. John B. Reeside, Jr., is nearly flat in cross section but has more convexity longitudinally. The brim is turned down rather sharply at the margin. The dorsal furrow is expressed by shallow furrows on the sides as far forward as the eyes; beyond that point there is only a faint indication of it. The eyes are in an elevated position. The anterior facial suture diverges slightly.



The librigenes have short slender genal spines.

Maurice formation; (loc. 26c) T. 30 N., R. 96 W., 6 miles south of Hailey, Wyoming.

*Holotype*.—U.S.N.M. No. 108700a; paratypes, Nos. 108700b, c.

**ARAPAHOIA POLITA, new species**

PLATE 7, FIGURES 10, 11

The cranidium, exclusive of the large occipital spine and posterolateral limbs, forms approximately a rectangle. A weakly defined dorsal furrow showing on the upper surface, probably is strongly indicated in exfoliated specimens. In cross section the cranidium is flatly arched but longitudinally the front third turns down rapidly. The eyes are of moderate size, situated at about the midpoint of the cranidium. Facial suture diverges slightly in front of the eye and rapidly behind the eye to form large posterolateral limbs. A broad, shallow furrow separates the greatly thickened neck ring which extends into a long, tapering, up-curved spine, the sides of which are strongly striated. No other parts have been assigned to the species.

Sullivan formation; (loc. 64h) East Lyell Glacier, 48 miles northwest of Lake Louise, Alberta.

*Holotype*.—U.S.N.M. No. 108701.

**ARAPAHOIA ELONGATA, new species**

PLATE 7, FIGURES 15-19, 32

This is a common species of the group found in this abundant fauna. It is characterized by a relatively narrow, long, tapering glabella which in exfoliated specimens is outlined by a shallow dorsal furrow. Fixigenes narrow. Eyes small. Facial suture diverges in front of eyes, then becomes intermarginal for a considerable distance, rounding the anterior angles. In cross section the head is flat, and longitudinally it has about the same flat curvature, except at the front edge, where it is rolled under slightly. The neck spine evidently was long. The librigena assigned to this species is rounded in contour on all edges, and in exfoliated specimens shows faint lines radiating from the eye. The pygidium assigned to the species is smooth and evidently has a punctate surface, but lacks a well-differentiated border.

Sullivan formation; (loc. 64h) East Lyell Glacier, 48 miles northwest of Lake Louise, Alberta.

*Holotype*.—U.S.N.M. No. 108703a; paratypes, Nos. 108703b, c.

**ARAPAHOIA ALBERTENSIS**, new species

PLATE 7, FIGURES 27-31

This is a very abundant species and is normal for the genus. Its outstanding characteristic is the enormous posterolateral limbs, which have pushed the rear facial suture forward nearly to the front margin of the glabella. In exfoliated specimens the glabella is clearly marked by four pairs of glabellar furrows. The shallow occipital furrow marks off a triangular neck ring extending into a long occipital spine. A tubercle near its base seems to be a median eye. Anterior facial suture diverges very little and evidently is intermarginal nearly to the center. The librigenae assigned to the species is short and stout, to fit with the contour of the facial suture. The pygidium assigned to the species is also short and has a well-defined border.

Sullivan formation; (loc. 64h) East Lyell Glacier, 48 miles northwest of Lake Louise, Alberta.

*Holotype*.—U.S.N.M. No. 108705a; paratypes, Nos. 108705b, c.

**ARAPAHOIA PROLIXA**, new species

PLATE 7, FIGURES 20-26

This large species is represented by a number of specimens. In length it resembles *A. elongata*. On exfoliated specimens the glabella is clearly defined and shows faint traces of glabellar furrows. The outer test has a keel. At the anterior end of the eye the fixigenae are narrow, measuring a little more than the width of the dorsal furrow. Anterior to the eyes the suture diverges, but less than in *A. elongata*. In cross section the species has low convexity, attained by an even curvature. Longitudinally it has greater convexity but this is also attained with even curvature. Concentric lines appear just behind the midpoint of the cranidium and possibly surround an eye. On the other hand, the brim is characterized by vertical anastomosing lines, which are stronger on exfoliated specimens. Unfortunately no examples are complete but a rather wide librigenae seems to represent the species. The pygidium assigned to the species is convex, with a fairly well-defined border. It has definite pleural furrows and grooves.

Sullivan formation; (loc. 64h) East Lyell Glacier, 48 miles northwest of Lake Louise, Alberta.

*Holotype*.—U.S.N.M. No. 108704a; paratypes, Nos. 108704b-d.

**ARAPAHOIA WALCOTTAE**, new species

PLATE 7, FIGURES 12-14

This is a short form similar to *A. albertensis*. In cranidia that retain the test the outline of the glabella is indicated by a shallow

dorsal furrow. Exfoliated specimens have the glabella much more sharply defined, and glabellar furrows are represented by pits. The eyes are slightly farther back than in *A. albertensis*. The suture diverges in front of the eye and forms large posterolateral limbs behind the eye. The middle portion of the brim projects somewhat. In cross section the cranidium has considerable elevation, attained by sharp curvature of the top of the glabella from which the posterolateral limbs bend downward with approximately the same slope. Longitudinally the species is not greatly curved.

Sullivan formation; (loc. 64e) East Lyell Glacier, 48 miles northwest of Lake Louise, Alberta.

*Holotype*.—U.S.N.M. No. 108702a; paratype, No. 108702b.

**PLETHOMETOPUS** Ulrich, 1930

**PLETHOMETOPUS ALBERTENSIS**, new species

PLATE 12, FIGURE 13

A single cranidium, typical of the genus in all respects is sufficiently well preserved to warrant naming. The simple large glabella, indicated by a faint dorsal furrow, is about three-fourths the length of the head, and tapers slightly to a rounded anterior margin. A strong occipital furrow separates a neck ring that extends into a short blunt spine. Fixigenes narrow, measuring at the eyes about a fifth the glabellar width. The posterolateral limbs are small and possibly short. Eyes small, situated about the midpoint of the glabella. In cross section the cranidium is rather evenly curved, while longitudinally the curvature is much greater, particularly in the anterior half. As a result the simple brim is convex in both directions. A faint broad anterior furrow is visible in the anterior angles.

Lyell formation; (loc. 20j) Tilted Mountain Brook, 9½ miles east of Lake Louise, Alberta.

*Holotype*.—U.S.N.M. No. 108755.

**KINGSTONIA** Walcott, 1924

**KINGSTONIA ELECTRA**, new species

PLATE 7, FIGURES 33-36

This species is represented by a number of cranidia, but thus far no pygidium which can be assigned to the species has been located. On the outer surface the cranidium shows few features. It is highly arched in both directions, becoming almost hemispherical. Indeed its outline departs slightly from a semicircle only by a flattening of the curvature at about the midpoint of the cranidial length. A narrow brim is present. Exfoliated specimens show a clearly defined glabella,

which extends to the anterior margin of the cranium. A narrow occipital ring is indicated.

Weeks formation; (locs. 30h, i) 5 miles south of Marjum Pass, House Range, Utah.

*Holotype*.—U.S.N.M. No. 108706a; paratypes, No. 108707.

**KINGSTONIA MUCRO**, new species

PLATE 8, FIGURES 1-8

This rather large species is represented by some 20 specimens. It is characterized by enormous posterolateral limbs, which give the cranium great width and cause it to depart from the more nearly semicircular outline of most species. The glabella is faintly indicated, more particularly in the rear where shallow furrows extend forward for some distance. There is a narrow rim of the usual type. The eyes are of normal size and situated somewhat in front of the mid-point. In cross section the head is strongly arched. The posterolateral limbs continue the downward slope, with increasing curvature near their distal ends. Longitudinally the cranium is highly arched. The associated pygidium, when viewed from the dorsal surface, has a rounded triangular shape. In profile it is very convex. At the anterior angles the sides stand vertical, but posteriorly the curvature increases until at the rear of the axis the pygidium is folded under. The axis is faintly outlined and in exfoliated specimens shows six rings. Pleural grooves are visible.

Sherbrooke limestone; (loc. 58f) ridge west of Mount Bosworth, British Columbia.

*Holotype*.—U.S.N.M. No. 108709a; paratypes, Nos. 108709a-d.

**KINGSTONIA BOSWORTHENSIS**, new species

PLATE 8, FIGURES 9-13

This species has normal size and shape. The cranium is quite globular with only short posterolateral limbs, and narrow brim around the front. In cross section the cranium stands very high with its greatest curvature toward the rear. Longitudinally it is curved rather evenly throughout, with a slight flattening in the front fourth. The associated pygidium is short and very convex.

Sherbrooke limestone; (loc. 57p) ridge west of Mount Bosworth, British Columbia.

*Holotype*.—U.S.N.M. No. 108710a; paratypes, Nos. 108710b, c.

**KINGSTONIA ROBSONENSIS, new species**

PLATE 8, FIGURES 14, 15

A single cranidium, fortunately rather well preserved, was found in the collection, showing that the Sullivan formation should be recognized in the Robson District. This cranidium is of average size and shape. The glabella is defined by a complete dorsal furrow, which shows as a darker line through the test but is not expressed as a furrow. A narrow striated brim is present and the posterolateral limbs are wide and bluntly rounded at the ends.

Sullivan formation; (loc. 61r) Moose River, 10 miles northeast of Robson Peak, British Columbia.

*Holotype*.—U.S.N.M. No. 108711.

**KINGSTONIA SULLIVANENSIS, new species**

PLATE 8, FIGURES 16-19

This globular species with rather large posterolateral limbs has a faintly defined glabella. A distinctly thickened and striated rim characterizes the holotype. The posterolateral limbs are rounded off abruptly.

Sullivan formation; (loc. 64m) Sullivan Peak, 48 miles northwest of Lake Louise, Alberta.

*Holotype*.—U.S.N.M. No. 108712a; paratypes, No. 108712b.

**KINGSTONIA PROMISSA, new species**

PLATE 8, FIGURES 20-23

Numerous cranidia and a few pygidia represent this species, which is slightly smaller than average. It is a short form with relatively wide fixigenes and large posterolateral limbs. The glabella is outlined only in the rear. In cross section the cranidium is very convex; the convexity being attained by the steeply inclined posterolateral limbs and a very sharp bending at the top of the glabella. Longitudinally the convexity is that of a quarter sphere. The pygidium is very plump, swelling greatly toward the rim.

Sullivan formation; (locs. 64c, j) Glacier Lake Canyon Valley, 48 miles northwest of Lake Louise, Alberta.

*Holotype*.—U.S.N.M. No. 108713a; paratype, No. 108713b.



**KINGSTONIA VULGATA**, new species

PLATE 8, FIGURES 26-30

This species is similar to *K. promissa*, differing in being less convex in every way, and having wider posterolateral limbs. It has normal convexity in both directions, in both the head and tail.

Sullivan formation; (loc. 64b) Glacier Lake Canyon Valley, 48 miles northwest of Lake Louise, Alberta.

*Holotype*.—U.S.N.M. No. 108715a; paratypes, Nos. 108715b, c.

**KINGSTONIA LOPERI**, new species

PLATE 8, FIGURES 24, 25

This species is represented by pygidia from several localities, but a sufficiently well-preserved cranidium to permit unquestioned determination has not been found. These fossils occur in very hard arkosic sandstone and quartzite; consequently not much can be done in the way of preparation. The illustrated specimen shows the quartz grains scattered through the siliceous matrix. Owing to its great length, this pygidium agrees rather well with that of *Bynumia*, but until positive evidence is available, it is placed in *Kingstonia*, the genus belonging to the horizon of the Sawatch fauna.

This pygidium has an elongate triangular shape, with a long, narrow axis clearly defined. Some of the exfoliated specimens, when weathered in a certain way, show the axial rings and the pleural furrows. On the exterior, however, only the anterior furrow and a faintly defined brim are visible. Further segmentation is shown but very faintly by reflection through the test.

Sawatch formation; (loc. 6a) Taylor Peak, 4 miles south of Ashcroft; (loc. 6) Italian Mountain, 15 miles northeast of Crested Butte, Colorado.

*Holotype*.—U.S.N.M. No. 108714.

**KINGSTONIA (?) PLENA**, new species

PLATE 8, FIGURES 31, 32

A single pygidium represents this large and tumid species. Since the pygidium is exfoliated the lateral portions of the dorsal furrow are fairly deep, but it is not traceable around the rear of the axis. The axis rises slightly above the pleural lobes, which slope gently from the dorsal furrow for about half their width, then turn down very rapidly. At the rear the entire pygidium has such great convexity

that the margin is turned under. At the rear the test is irregularly striated.

Sullivan formation; (loc. 64h) East Lyell Glacier, 48 miles northwest of Lake Louise, Alberta.

*Holotype*.—U.S.N.M. No. 108716.

### KINGSTONIA ARA (Walcott)

PLATE 8, FIGURES 42-46

*Ucebia ara* WALCOTT, Smithsonian Misc. Coll., vol. 75, No. 2, p. 60, pl. 14, fig. 4, 1924; *ibid.*, No. 3, p. 118, pl. 17, figs. 7, 8, 1925.

*Kingstonia ara* RESSER, *ibid.*, vol. 95, No. 4, p. 24, 1936.

In addition to the holotype and paratype cranidia that are refigured, another specimen from the type locality is added to show the changed aspect resulting from exfoliation. It will be remembered that the genus *Ucebia* was erected on this species, because the glabella was well defined. However, as the illustrations show both exfoliated specimens and one cranidium retaining part of the test, it is clear that *Ucebia* is not a valid genus. When the shell is removed, any species of *Kingstonia* becomes *Ucebia*.

The locality erroneously stated in the original description, is given correctly below.

Warrior limestone; (loc. 24f) 1 mile southeast of Warriors Mark, Pennsylvania.

*Holotype*.—U.S.N.M. No. 70257; paratype, No. 70258; plesiotype, 108720.

### KINGSTONIA KINDLEI, new species

PLATE 9, FIGURES 1-4

This species is named for Dr. Cecil Kindle, who collected the cranidium and several pygidia from the belt of Warrior limestone exposed in the southwestern portion of the Bellefonte quadrangle.

*K. kindlei* differs somewhat from *K. ara* (Walcott), which occurs in the same limestone belt to the southwest in the Tyrone quadrangle. It averages larger and is more convex than *K. ara*. Also the anterior outline is more circular. The holotype cranidium retains the test, and consequently the dorsal furrow can be seen only when the specimen is held so that strong cross light falls parallel to the slope of the glabella and fixigene. A narrow striated rim is set in a nearly vertical position. In cross section this cranidium is very high with a nearly even curvature. When viewed from the side, the cranidium appears to be a quarter sphere. The associated pygidium has a nearly cylin-

dricul axis, which extends almost to the rear margin. Posteriorly it coalesces with the pleural lobes, owing to shallowing of the dorsal furrow.

Warrior limestone; (loc. 38e) 1 mile northwest of Benore, and 5 miles west of State College, Pennsylvania.

*Holotype*.—U.S.N.M. No. 108721a; paratypes, Nos. 108721b, c.

#### BYNUMIA Walcott, 1924

*Bynumia* WALCOTT, Smithsonian Misc. Coll., vol. 75, No. 2, p. 54, 1924; *ibid.*, No. 3, p. 78, 1925.

The additional species here described add proof that *Bynumia* is a valid genus. Examples of the librigenae and pygidium are also added to the genus. The illustrations show that the glabella of *Bynumia*, like that of *Kingstonia*, is clearly marked in exfoliated cranidia, but in unexfoliated examples it is seldom indicated by more than a suggestion of the dorsal furrow.

*Genotype*.—*B. eumus* Walcott (restricted).

#### BYNUMIA EUMUS Walcott

##### PLATE 9, FIGURES 5-7

*Bynumia eumus* WALCOTT, Smithsonian Misc. Coll., vol. 75, No. 2, p. 54, pl. 10, fig. 2, 1924; *ibid.*, (part) No. 3, p. 78; pl. 17, fig. 4, 1925.

A pygidium is figured in addition to the holotype cranidium. Because the number, poorly written on the type cranidium, was misread, its locality was erroneously given in the Sawback Range.

Sullivan formation; (loc. 64b) head of Glacier Lake Canyon Valley, 48 miles northwest of Lake Louise, Alberta.

*Holotype*.—U.S.N.M. No. 70255; plesiotype, No. 108722.

#### BYNUMIA ELEGANS, new species

##### PLATE 9, FIGURES 8-12

This species, represented by a large number of specimens, is close to *B. eumus*, and hence typical of the genus in all respects. In *B. elegans* the glabella is rather slender and more truncate than usual. Its distinguishing characteristics, as in other species, reside chiefly in the proportions of the brim. The brim width is equal to half the glabellar length and comes to a sharper point than in *B. eumus*. Another difference from that species is found in the occipital furrow, which extends on to the posterolateral limbs. These limbs are further

distinguished by their convexity. The associated pygidium is similar to that of *B. eumus*, differing chiefly in somewhat greater relief of the axis and the portions near the margin, particularly toward the rear.

Sullivan formation; (loc. 64r) Ranger Brook Canyon, Sawback Range, Alberta.

*Holotype*.—U.S.N.M. No. 108723a; paratypes, Nos. 108723b-d.

#### **BYNUMIA ARGUTA, new species**

PLATE 9, FIGURES 13-15

This species is represented by several examples. Its fairly wide glabella is square in front and rounded at the anterior angles. As a whole the outline is nearly that of an equilateral triangle. A shallow dorsal furrow, visible on the exterior, separates the brim from the glabella. The brim is considerably swollen in front. From the front the cranidial cross section is little curved, except at the outer edges. Since the posterolateral limbs are greatly depressed in the rear, the cranidium is highly arched. Longitudinally the curvature is moderate, except at the very front, where the swollen rim drops steeply. The associated pygidium is flat and so fused that the axis is scarcely traceable.

Sullivan formation; (loc. 66s) Badger Pass, Sawback Range, Alberta.

*Holotype*.—U.S.N.M. No. 108724a; paratype, No. 108724b.

#### **BYNUMIA WALCOTTI, new species**

PLATE 9, FIGURES 16-20

*Bynumia eumus* WALCOTT (part), Smithsonian Misc. Coll., vol. 75, No. 3, pl. 17, figs. 5, 6, 1925.

This species was included by Walcott in *B. eumus*, which it resembles. It is abundantly represented at several localities by many specimens. Compared with *B. eumus*, *B. walcotti* appears to be a stockier form, particularly when not exfoliated. This appearance is due to the more convex and slightly narrower brim. The pygidium assigned to the species is flat, with the poorly defined axis raised slightly above the flat pleural lobes.

Sullivan formation; (loc. 66m) 5 miles northwest of Banff, and (loc. 66s) Badger Pass, Sawback Range, Alberta.

*Holotype*.—U.S.N.M. No. 108731a; paratypes, Nos. 70256, 108731b.

**BYNUMIA VENUSTA**, new species

PLATE 9, FIGURES 21-28

This abundantly represented species is characterized chiefly by its narrow cranial shape, which forms an isosceles triangle. Longitudinally the curvature is not great, and the relatively wide brim continues the gradual slope of the anterior portion of the glabella. The librigena figured, the first for the genus, constitutes almost a quarter circle, the outer margin increasing its rate of curvature toward the genal angle. Several pygidia are figured, one with a complete test and two partially exfoliated examples. The latter show how the axial rings and pleural furrows and grooves are developed on the under side of the test.

Sullivan formation; (loc. 64s) Ranger Brook Canyon, Sawback Range, Alberta.

*Holotype*.—U.S.N.M. No. 108725a; paratypes, Nos. 108725b-f.

**BYNUMIA ROBSONENSIS**, new species

PLATE 9, FIGURES 30-34

One species of *Bynumia* occurs in the Robson District, far north of the localities of the other species. This species is characterized by its triangular outline, with the base being longer than the sides. The photographs fail to bring out the sharpness of the brim, owing to the high convexity developed near the tip.

Lynx formation (Sullivan equivalent); (locs. 19m, L) Iyatunga Mountain, Mount Robson, British Columbia.

*Holotype*.—U.S.N.M. No. 108726a; paratypes, Nos. 108726b, c.

**BYNUMIA SULCATA**, new species

PLATE 9, FIGURES 35, 36

A single small distinctive cranium has the usual triangular outline and average shape of other species in the Sawback Range. Because of the depth of the dorsal furrow, *B. sulcata* is closest to *B. arguta*, but carries this development much further. Not only is the dorsal furrow deeply impressed both on the sides and in front, but in addition, the brim, set in a nearly horizontal position, does not continue the glabellar slope. This is a remarkable development in a specimen that is not completely exfoliated. The side view shows the distribution of convexity.

Sullivan formation; (loc. 64s) Ranger Brook Canyon, Sawback Range, Alberta.

*Holotype*.—U.S.N.M. No. 108727.



**BYNUMIA RANGERENSIS**, new species

PLATE 9, FIGURES 37-41

This well-represented species is allied to *B. cumus* in size and proportions of the glabella. In cross section the brim, and to a lesser degree the glabella and posterolateral limbs, are highly convex. Longitudinally the convexity is not great, except in the swollen brim. The brim width is less than half the glabellar length. The rather large associated pygidium is nearly flat in cross section, but in the opposite direction has increasing curvature in the posterior moiety.

Sullivan formation; (loc. 66L) Ranger Brook Canyon, Sawback Range, Alberta.

*Holotype*.—U.S.N.M. No. 108728a; paratypes, Nos. 108728b, c.

**BYNUMIA SAWBACKENSIS**, new species

PLATE 9, FIGURES 42-44

This large, well-represented species is characterized particularly by its wide brim, which exceeds half the glabellar length. Not only is the brim wide, but when viewed from the front comes to a blunt, nearly cylindrical point. The pygidium has a blunt rear margin, reached by the faintly outlined axis.

Sullivan formation; (loc. 64w) Ranger Brook Canyon, Sawback Range, Alberta.

*Holotype*.—U.S.N.M. No. 108729a; paratype, No. 108729b.

**BYNUMIA (?) MODESTA**, new species

PLATE 8, FIGURES 33, 34

This species lies between *Bynumia* and *Kingstonia* and should possibly be referred to the latter genus.

The glabella is large and relatively wide, so that it occupies by far the greater portion of the cranium. The front outline is strongly curved but does not come to such a sharp point as in other species. Longitudinally the cranium is convex with an even curvature. It is also convex laterally, but this convexity is attained by a sharp bend along the median line causing the glabella and posterolateral limbs, as well as the palpebral lobes, to slope down sharply on each side. The steeply inclined halves of the cranium are only a little curved in themselves. The eyes are small and are situated well forward. A narrow rim is visible in front.

Sullivan formation; (loc. 64h) Glacier Lake Canyon Valley, 48 miles northwest of Lake Louise, Alberta.

*Holotype*.—U.S.N.M. No. 108717.

**BYNUMIA (?) PRODUCTA, new species**

PLATE 8, FIGURES 35, 36

Although this species is represented by many specimens, only one cranidium is figured. In its relatively flat anterior outline and somewhat upturned, thickened rim, and in the lack of divergence of the anterior facial suture, this species resembles *Blountia*. However, since the fixigenes are almost triangular in shape, it is placed in *Bynumia*.

Owing to the truncate anterior outline, the glabella is more quadrate than usual. The very shallow dorsal furrow converges slightly forward and rounds off the anterior angles. A shallow occipital furrow outlines a narrow ring. A deep depression crosses the preglabellar area in front of the glabella, and the rim is thickened, so that it is rather prominent in side view.

Numerous pygidia are in hand, but because the specific association is rather uncertain they have not been definitely assigned to the species. These pygidia are characterized by the usual triangular shape, axial and other features, differing from *B. mollis* chiefly in the abrupt slopes along the outer margin, which are so steep that the edges are rolled over.

Sullivan formation; (loc. 64i) Glacier Lake Canyon Valley, 48 miles northwest of Lake Louise, Alberta.

*Holotype*.—U.S.N.M. No. 108718.

**BYNUMIA MOLLIS, new species**

PLATE 8, FIGURES 37-41

A few specimens characterized by a pronounced triangular shape represent this species. The glabella is faintly outlined on the sides by the dorsal furrow and in front by a change in slope. The thickened rim is slightly upturned. Viewed from the rear, the glabella stands above the posterolateral limbs, owing to deep notching of the posterior margin at the ends of the dorsal furrow. Viewed from the front, the lateral curvature is rather even, with the greatest amount along the median line. Longitudinally the nearly even curvature of the glabella is interrupted by the more horizontal position of the brim. The pygidial axis is long, slender, and tapers gradually, reaching nearly to the rear margin. A faint border is visible, and on exfoliated specimens the usual segmentation is clearly defined both in the axis and the pleural lobes.

Sullivan formation; (loc. 64h) East Lyell Glacier, 48 miles northwest of Lake Louise, Alberta.

*Holotype*.—U.S.N.M. No. 108719a; paratypes, Nos. 108719b, c.

**BYNUMIELLA**, new genus

It appears that the *Bynumia* stock continued into Franconia time, taking on a somewhat changed form. The alterations in structure may be summed up by stating that they are modifications of *Bynumia* in the direction of average trilobite structure. For instance, the brim structure is retained, but with modification in the direction of reduction to the more normal band form. Likewise the glabella develops considerable taper, the dorsal furrow becomes deeper and an occipital furrow separates a neck ring, which is expanded backward in the middle. Only cranidia are known.

*Diagnosis*.—Small trilobites with a tapering glabella without furrows. Dorsal and occipital furrows are well defined. The simple brim varies in width, but tends to extend forward in the middle, causing the anterior outline of the cranium to project.

*Genotype*.—*B. typicalis*, new species.

**BYNUMIELLA TYPICALIS**, new species

PLATE 10, FIGURES 1, 2

Several small cranidia have been located in the collection, characterized by a glabella which tapers to a rounded point, and which is demarcated by the well-defined dorsal furrow. An equally deep occipital furrow separates a swollen neck ring. The fixigenes average about the same width as the brim, and the latter has a width equal to one-third the glabellar length. The eyes are small, situated well forward.

Lyell formation; (loc. 66j) Northeast branch Ranger Brook Canyon, 10 miles northwest of Banff, Sawback Range, Alberta.

*Holotype*.—U.S.N.M. No. 108732a; paratype No. 108732b.

**BYNUMIELLA BRISCOENSIS**, new species

PLATE 9, FIGURE 29

Several cranidia from the Sabine formation represent *Bynumiella*. In the holotype cranium the glabella tapers to a rounded front less sharp than in *B. typicalis*. The brim width is somewhat less than one-third the glabellar length. Owing to depression of the anterior angles, the brim is convex. The cranium is moderately arched in both directions.

Sabine formation; (loc. 16t) Sinclair Canyon, Brisco Range, British Columbia.

*Holotype*.—U.S.N.M. No. 108730.

**BYNUMIELLA (?) OKLAHOMENSIS, new species**

PLATE 10, FIGURES 27, 28

Pending the availability of better material several cranidia that are not fully typical are referred to the genus. This species differs from typical forms in that the glabella tapers less rapidly and in the size and position of the eyes, which are far larger and situated much farther back than they should be for a *Bynumiella*. Brim, occipital ring, and fixigenes are all typical.

The illustrations show the characteristics of the holotype cranidium. Faint glabellar furrows are present. A thickening of the neck ring produces a short blunt spine. Longitudinal curvature is shown in figure 27, and that in the opposite direction is about the same.

Signal Mountain formation; (loc. 201j) 1 mile south of Royer Ranch, Arbuckle Mountains, Oklahoma.

*Holotype*.—U.S.N.M. No. 108743.

**BYNUMINA, new genus**

A second genus *Bynumina* is erected for the *Bynumia* stock that continued into Franconia time. As in *Bynumiella* this genus represents development of *Bynumia* in the direction of more average trilobite structure. Although glabellar taper was an essential change in this instance, the head as a whole is less constricted anteriorly. Glabellar furrows also appear, but the most pronounced change lies in the brim structure, which brings that part more nearly to form a transverse band.

*Diagnosis*.—Small trilobites characterized by large, somewhat tapered glabella. Dorsal and occipital furrows well defined. Glabellar furrows faint. Neck ring narrow and of even width throughout. Eyes small, situated well forward. Brim simple, of nearly even width throughout. Faint eye lines present. Pygidium simple; axis long, tapered, poorly defined, and with faint axial rings. Pleural lobes completely fused.

*Genotype*.—*B. caelata*, new species.

**BYNUMINA CAELATA, new species**

PLATE 10, FIGURES 18-22

Numerous cranidia and one pygidium represent this species. The illustrations show both the generic and specific characteristics.

The glabella tapers gradually to a truncated front margin. The anterior corners are rounded, and along the sides the dorsal furrow

bows outward slightly. Several pairs of recurved glabellar furrows are visible. The occipital furrow, both on the glabella and fixigenes, is deeply impressed. In cross section the cranidium is convex, reaching the greatest curvature as the median line is approached. Longitudinally the convexity is less, and the rate of curvature even throughout. The brim width is a little more than one-fourth the glabellar length, and is a simple convex band surrounding the front of the head. The associated pygidium is also convex, with a broad, faintly outlined axis and fused pleural lobes.

Davis formation; (loc. 92d) Federal Lead Mine No. 4, Flat River, Missouri.

*Holotype*.—U.S.N.M. No. 108740a; paratypes, Nos. 108740b-d.

**BYNUMINA MISSOURIENSIS**, new species

PLATE 10, FIGURES 23-26

This is the more common Missouri species, and it differs from *B. caelata* mainly in its narrower rim.

*B. missouriensis* has a tapering glabella, but the curvature of the lateral dorsal furrows is not even. It expands rapidly as far forward as the first glabellar furrow, then suddenly begins to contract, maintaining a nearly straight course until it approaches the anterior angles, where the rate of taper becomes less again. Besides this peculiarity, the species is characterized by a rim width of a little more than one-fifth the glabellar length.

Davis formation; (locs. 11k, 91y) Flat River, Missouri.

*Holotype*.—U.S.N.M. No. 108741; paratypes, Nos. 108742a, b.

**STENOPILUS** Raymond, 1924

**STENOPILUS BACCA**, new species

PLATE 10, FIGURES 8-13

Such a featureless hemispherical trilobite as *Stenopilus* is difficult to describe. Several species are here presented, chiefly to show the differences between small and large examples, and the variation in degree of sphericity. There seems to be little doubt but that these trilobites developed from a *Kingstonia* ancestor.

Large cranidia of *S. bacca* are nearly hemispherical in shape, but, as may be seen in figures 10 and 11, small heads show a distinct *Kingstonia* shape. Of course, the indentations of the dorsal furrow in the rear remain, but unless the very convex specimen is specially posed, they are obscured by the bulging cranidium.



Signal Mountain formation; (locs. 12i, j) 2 miles southwest of Signal Mountain, Wichita Mountains, Oklahoma.

*Holotype*.—U.S.N.M. No. 108737; paratypes Nos. 108738a-c.

**STENOPILUS ADUNCUS, new species**

PLATE 10, FIGURES 14-17

A second species is chosen for description to show the elongate form taken by species of *Stenopilus*. This development recalls the *Bynumia* elongation of the *Kingstonia* stock, but in *Stenopilus* this attends obesity and elimination of all furrows. As a result a smooth trilobite is developed, so convex that the glabella overhangs the posterior margin. This high convexity is reduced forward, but the curvature is not eliminated in any portion of the test.

*S. aduncus* is longer than wide and has its greatest convexity at the rear. Otherwise it is practically featureless.

Signal Mountain formation; (loc. 12L) Pickens Ranch, Arbuckle Mountains, Oklahoma.

*Holotype*.—U.S.N.M. No. 108739a; paratype, No. 108739b.

**BLOUNTIA Walcott, 1916**

**BLOUNTIA PLANA, new species**

PLATE 14, FIGURES 12-14

Only pygidia have been assigned to the species. While the long axis is defined, and the usual interrupted axial furrows are visible, it does not stand above the pleural lobes. The chief characteristic of the species is found in the flatness of the pygidium. When viewed from the rear, the pleural platforms, with the axis, form only a slightly convex shield. The border is slightly concave, thereby increasing the curvature near the lateral margins.

Sullivan formation; (loc. 64c) Glacier Lake Canyon Valley, 48 miles northwest of Lake Louise, Alberta.

*Holotype*.—U.S.N.M. No. 108779a; paratype, No. 108799b.

**BLOUNTIA KINDLEI, new species**

PLATE 14, FIGURES 27-31

Two small pygidia and a portion of the cranidium are figured. A somewhat broken pygidia is included to show appearance of the test; one much larger pygidium has not been figured. This species, which is named in honor of the collector, Dr. Cecil Kindle, is typical of the genus in every respect.

The large glabella tapers at a normal rate to the rounded front. It lacks furrows and even the occipital furrow is very faint. The fixigenes average less than half the glabellar width, expanding to the moderate anterior angles, and behind the eye into stout posterolateral limbs. Eyes are small, situated about the midpoint of the cranidium. The rather heavy, somewhat upturned rim is about the same width as the preglabellar area. When exfoliated, the pygidium shows a long axis on which at least six rings are faintly indicated. As a whole, the pygidium is triangular in outline. In cross section the curvature is gentle, except near the margins where the slope increases so much that the outer edges are slightly turned under.

Warrior limestone; (loc. 38e) 1 mile northwest of Benore, 5 miles west of State College, Pennsylvania.

*Holotype*.—U.S.N.M. No. 108788a; paratypes, Nos. 108788b, c.

#### **BLOUNTIA (?) DISPARILIS, new species**

PLATE 14, FIGURES 10, 11

This narrow cranidium is not typical of *Blountia*. The glabella tapers to a rounded anterior outline and lacks glabellar furrows. A shallow occipital furrow separates a narrow neck ring. The fixigene is narrow, averaging about one-third the average glabellar width. The wide brim is subdivided into a preglabellar area and a wider rim. The rim is thickened and increases in the middle to about twice the width of the preglabellar area. Eyes small. Longitudinally the cranidium attains considerable convexity by rather strong curvature in the rear portion. In cross section the curvature, including the posterolateral limbs, is more even.

Sullivan formation; (loc. 64h) Glacier Lake Canyon Valley, 48 miles northwest of Lake Louise, Alberta.

*Holotype*.—U. S. N.M. No. 108775.

#### **BLOUNTIELLA Resser, 1938**

##### **BLOUNTIELLA ALBERTA, new species**

PLATE 14, FIGURES 19-26

Although this species is represented by numerous cranidia, the pygidium has not been located. Taken as a whole, the cranidium is rather short, and the glabella occupies most of its cranial area. Glabellar furrows are lacking even in exfoliated specimens. The fixigenes average less than half the glabellar width. The eyes are small, situated about the midpoint of the cranidium. A narrow preglabellar

area separates the thickened, striated rim from the dorsal furrow. Laterally the head is moderately and evenly convex, but longitudinally the curvature is much greater. A shallow occipital furrow separates a narrow ring.

Sullivan formation; (locs. 64c, b) Glacier Lake Canyon Valley, 48 miles northwest of Lake Louise, Alberta.

*Holotype*.—U.S.N.M. No. 108776a; paratypes, Nos. 108776b, 108777a, b.

#### ELLIPSOCEPHALOIDES Kobayashi, 1935

*Ellipsocephaloides* KOBAYASHI, Journ. Fac. Sci. Imp. Univ. Tokyo, sect. 2, vol. 4, pt. 2, p. 196, 1935.

This generic name was assigned without proper study of the specimens, for it perpetuates the false idea of relationship between these trilobites and *Ellipsocephalus*. The species of *Ellipsocephaloides*, moreover, are unique in several respects, and could not belong to the *Iliaenuridae*, which should have been apparent even before the pygidium was known. Under present circumstances the best procedure is to place the genus in a new family, leaving the determination of the family's position in trilobite classification to future study.

Considerable variation in width of the anterior fixigene and the more advanced course of the facial suture due to a more forward position of the eye may be observed among the species here described. Though these variations fall almost entirely on one side of the genotype, *E. curtus* (Whitfield), the narrow forms and those in which the eye is farther back are not segregated as a separate genus since sufficient gradation seems to exist to tie all together. *Ellipsocephaloides* is apparently characteristic of Franconia horizons, for it is associated with *Idahoia*, *Pseudagnostus*, *Briscoia*, and other genera of Franconia age.

Species of *Ellipsocephaloides* vary considerably in shape. The glabella is large and clearly defined, both by the dorsal furrow and its elevation above the fixigenes. Some species have three pairs of short glabellar furrows. Occipital furrow always developed, marking off a neck ring, usually of even width throughout. Brim a simple band, except in the wider species where a narrow rim is demarcated by a shallow anterior furrow. The brim continues as the anterior fixigene around the anterior angles and therefore curves much more sharply in the narrow than in the wide forms. At their widest point the fixigenes, exclusive of the eye band, vary from less than half to more than the glabellar width at the same point. Fixigenes between the dorsal furrow and the eye are usually nearly flat, though they may

be concave. Since the very heavy eye bands are elevated, most of the fixigene may lie below the level both of the dorsal furrow and of the eye. The moderate-size eyes vary considerably in position. Libragene unknown.

Pygidium characterized by a stout axis in which two or more segments are indicated. The axis is from a half to two-thirds the length of the pygidium and stands above the dorsal furrow. Pleural lobes flat, extending fanwise into marginal spines. Pleural furrows strong and pleural grooves usually visible. Marginal spines usually rather blunt, forming a serrate edge. As the genus is now constituted they number from one to five on a side, depending on the degree of fusion.

**ELLIPSOCEPHALOIDES ARGUTUS, new species**

PLATE 10, FIGURES 5, 6

Several cranidia from the Ram Creek area retain sufficient of their characters to warrant description. The cranidium is broad. The almost parallel-sided glabella extends nearly the full length of the cranidium. In cross section it stands entirely above the shallow dorsal furrow and the fixigenes which slope gently down from it. The occipital furrow is clearly defined both on the glabella and fixigenes, and three pairs of glabellar furrows are traceable. The fixigenes between the eyes and the dorsal furrow are about as wide as the glabella at the same point. Unfortunately the eyes are not completely preserved, but appear to have been of normal size, shape and position.

Sabine formation; (loc. 12s) Ram Creek, 15 miles south of Canal Flats, British Columbia.

*Holotype*.—U.S.N.M. No. 108735a; *paratype*, No. 108735b.

**ELLIPSOCEPHALOIDES BRISCOENSIS, new species**

PLATE 10, FIGURE 7

One of a dozen or more cranidia is figured. *E. briscoensis* is narrower than *E. argutus* from the same region. Because of this feature it bridges the gap between the genotype and the narrow forms. The glabella is rectangular with rounded anterior angles and has two or three pairs of glabellar furrows represented by elongate pits. In width the brim measures less than a fourth the glabellar length. It has a peculiar narrow elevation in the middle, and also has a faintly defined narrow rim. As a whole the brim is slightly convex and is set in a horizontal position. On the sides the brim passes into the anterior fixigenes which maintain its level. In fact the outer margins of the fixigenes are curved up and back to the genal angles so that

the ocular platforms are depressed, leaving the eye lobes in a prominent position. In this species the eyes are long, and the eye bands wide and heavy. Faint eye lines extend straight across the fixigenes slightly anterior to the second pair of glabellar furrows.

Sabine formation; (loc. 17s) Sabine Mountain, Brisco Range, British Columbia.

*Holotype*.—U.S.N.M. No. 108736.

**ELLIPSOCEPHALOIDES SILVESTRIS, new species**

PLATE 11, FIGURES 1-3; PLATE 12, FIGURE 7

This form, intermediate between the broad and narrow species, is well represented in the collections. The nearly quadrate glabella is a little longer than wide and is well rounded in front. The occipital ring is of even width. The fixigenes are less than half the glabellar width and maintain their width throughout. The simple brim, only a little narrower than the fixigenes, has an elongate boss in the middle. A narrow rim is faintly indicated for a short distance in the middle of the head. Wide eye lines connect the wide eye lobes with the dorsal furrow.

The associated pygidium has a short wide axis on which three or four rings are demarcated. The pleural lobes and the rear border, which is as wide as the axis is long, have both pleural grooves and furrows. Both extend to the margin, producing sharp ridges. Five spines are developed on each side.

Honey Creek limestone; (loc. 91b) West Timbered Hills, Arbuckle Mountains, Oklahoma.

*Holotype*.—U.S.N.M. No. 108744a; paratypes, Nos. 108744b-d.

**ELLIPSOCEPHALOIDES SAWBACKENSIS, new species**

PLATE 11, FIGURES 4, 5

Only the two cranidia illustrated represent this distinctive species. The glabella is longer than wide and has three pairs of glabellar furrows indicated by pits. The fixigenes are about half the glabellar width and vary little from front to back. Heavy eye lines connect the large elevated eye bands with the dorsal furrow at a point in front of the anterior pair of glabellar furrows. The brim, about half the width of the fixigenes, is simple in structure but is raised as a boss in the center.

Lyell formation; (loc. 64x) Ranger Brook Canyon, Sawback Range, Alberta.

*Holotype*.—U.S.N.M. No. 108745a; paratype, No. 108745b.



**ELLIPSOCEPHALOIDES CARUS, new species**

PLATE II, FIGURES 7, 8

This is a small form associated with *E. argutus*.

The subcylindrical glabella is rounded in front and has three pairs of glabellar furrows. The fixigenes are convex in contrast to most other species; consequently the rather thin eye lines appear to be more curved than usual. The eyes are on slightly upturned heavy bands.

Sabine formation; (loc. 12s) Ram Creek, 15 miles south of Canal Flats, British Columbia.

*Holotype*.—U.S.N.M. No. 108747a; paratype, No. 108747b.

**ELLIPSOCEPHALOIDES MONTIS, new species**

PLATE II, FIGURES 9-11

The third species from the locality is an intermediate form, approaching the narrow rather than the broad species. Width may be an aspect as much as a reality, since the narrowness in dorsal view is sometimes due to the sloping position of the anterior angles, whereas other species appear wider because the anterior flanges of the same size are more nearly in a horizontal position. The wide glabella of *E. montis* is well rounded in front, and has a slight indentation at the center. Glabellar furrows are reduced to faint pits. The most distinctive feature is the fusing of the broad eye line with the brim, which slopes back to the eyes, the latter being in a posterior position. This gives the cranidium the appearance of being made up of the large glabella about which is draped a wide band that slopes toward the rear. Anterior fixigenes are eliminated by this juncture of the eye ridge and brim. Between the eyes and glabella the fixigenes have just a little more than one-third the glabellar width. In this species the neck ring is rather wide.

Sabine formation; (loc. 12s) Ram Creek, 15 miles south of Canal Flats, British Columbia.

*Holotype*.—U.S.N.M. No. 108748a; paratype, No. 108748b.

**ELLIPSOCEPHALOIDES BEARENSIS, new species**

PLATE II, FIGURE 12

An imperfect cranidium represents the genus in the St. Charles formation of Idaho, showing that this element is also present in that fauna. This species is much more like the genotype in general aspect, but differs distinctly owing to the more posterior position of the eyes. Glabellar furrows seem to be lacking. The eye lines are very much

reduced, consisting only of a slightly elevated portion of the fixigenes. The eye band is turned up but does not have a distinct palpebral furrow.

St. Charles limestone; (loc. 66z) 5 miles west of St. Charles, Bear River Range, Idaho.

*Holotype*.—U.S.N.M. No. 108749.

**ELLIPSOCEPHALOIDES BUTLERI, new species**

PLATE 11, FIGURES 14, 15

This species, represented by numerous cranidia, is preserved in sandstone, and is associated with *Briscoia*. It has a typical development for the genus but is not proportionally as wide as the genotype. Glabellar furrows are present but may be lacking on the test. The eyes are strongly bowed and situated about the middle of the cranidium.

Sawatch formation; (loc. 37x) near Gilman, Mosquito Range, Colorado.

*Holotype*.—U.S.N.M. No. 108751a; paratype, No. 108751b.

**ELLIPSOCEPHALOIDES NITELA, new species**

PLATE 11, FIGURE 13; PLATE 12, FIGURES 1-3

This narrow form, represented by many examples, most resembles *E. silvestris*. Compared with that species *E. nitela* is somewhat broader and in the pygidium the pleura are wider. The nearly quadrate glabella has rounded anterior angles. The fixigenes are less than half the glabellar width, and are a little wider than the brim. The eye lines are weak and the broad eye bands are clearly defined by the palpebral furrows. The simple brim has a slight elevation in the middle. The associated pygidium has a broad axis on which the furrows are deep. In cross section the axis stands above the pleural lobes, which retain both the pleural grooves and furrows. The latter bisect the pleura obliquely, decreasing in strength posteriorly. Four marginal spines, decreasing in size from front to back, terminate the four pleural segments.

Honey Creek limestone; (loc. 12m) 7 miles north of Springer, Arbuckle Mountains, Oklahoma.

*Holotype*.—U.S.N.M. No. 108750a; paratypes, Nos. 108750b-d.

**ELLIPSOCEPHALOIDES MONSENSIS, new species**

PLATE 12, FIGURES 4-6

This narrow species similar to *E. montis* is represented by a number of cranidia and the pygidium. The quadrangular glabella is about

a third longer than wide, and has several pairs of glabellar furrows. The brim is narrower than the neck ring, a characteristic common to several of the Canadian species. The brim joins the eye ridges, which also form a raised band. The rather large eyes are situated well forward. The fixigenes, less than half the glabellar width, contract forward to meet the relatively narrow brim.

A beautiful pygidium with a wide flaring border bears two spines on each side. Its short, wide axis extends into a long postaxial ridge. Only two axial rings and pleura are defined. The entire pygidium is covered by prominent anastomosing lines.

Lyell formation; (loc. 64f) Mons Glacier, 50 miles northwest of Lake Louise, Alberta.

*Holotype*.—U.S.N.M. No. 108752a; paratype, No. 108752b.

#### ELLIPSOCEPHALOIDES DECLIVIS, new species

PLATE 12, FIGURES 10-13

This species is represented by several cranidia. It is similar to *E. monensis* except for the more posterior position of the eyes. The long, parallel-sided glabella is rounded in front, and in cross section stands completely above the palpebral lobe. The rear pair of glabellar furrows is continuous across the glabella and one shallow pair is visible anterior to it. The fixigenes, measuring less than half the glabellar width, slope down steeply from the dorsal furrow, though at a lesser angle than the sides of the glabella. The eyes are of normal size and are connected by a thickened eye ridge with the narrow convex brim.

Lyell formation; (loc. 20j) Tilted Mountain Brook,  $9\frac{1}{2}$  miles east of Lake Louise, Alberta.

*Holotype*.—U.S.N.M. No. 108754a; paratype, No. 108754b.

#### MARYVILLIA Walcott, 1916

##### MARYVILLIA WYOMINGENSIS (Resser)

PLATE 12, FIGURES 14-20; PLATE 14, FIGURE 1

*Bathyriscus* sp., WALCOTT, U. S. Geol. Surv. Monogr. 32, p. 466, pl. 64, fig. 6, 1899.

*Coosia wyomingensis* RESSER, Smithsonian Misc. Coll., vol. 95, No. 22, p. 7, 1937.

Heads and tails of a species of *Maryvillia* occur throughout the Yellowstone Park region ranging from Clark Fork, Wyoming, to the Castle Mountains, Montana. A good cranidium on the hand specimen with the holotype of *Tricrepicephalus tripunctatus* (Whitfield) comes from Moss Agate Springs in the Castle Mountains, Montana.

The glabella tapers slightly to a rounded front. At the eye the fixigenes are exactly half the glabellar width. The facial suture forms rather broad posterolateral limbs. Eyes small and strongly bowed. Brim concave, with a rim differentiated by a change in slope. Eye lines traceable on exfoliated specimens.

Pygidium convex, sloping down rather sharply at the anterior angles. Outer test smooth, and dorsal furrow shallow. On exfoliated specimens both the pleural furrows and grooves are visible.

Pilgrim formation; Dead Indian Creek; and (loc. 151g) mouth of Clark Fork River, Absaroka Range, Wyoming; (loc. 4r) Suce Creek, Mount Delano, Snowy Range; and near Moss Agate Springs, Castle Mountains (with type of *Tricrepiccephalus tripunctatus*), Montana.

*Holotype*.—U.S.N.M. No. 94343; plesiotypes, Nos. 108756, 108757, 108772.

**MARYVILLIA VIOLAENSIS, new species**

PLATE 12, FIGURES 21-26

About a dozen cranidia and half as many pygidia have been located in the collections. Only two small cranidia are illustrated, as all the larger specimens are incomplete.

Two partially preserved cranidia show that the cranidium of the species attained a length of about 15 mm. and a width of about 25 mm. The glabella is poorly defined because the dorsal furrow is very shallow. Eyes, eye lines, and fixigenes are average in development. The brim on the other hand is excessively concave, and consequently the rim seems to be more distinct than usual. As a whole the cranidium is gently convex in a transverse direction and much more sharply convex longitudinally.

In the pygidium the axis is clearly outlined by a shallow dorsal furrow. Axial rings and the anterior pleural furrows are faintly indicated. The pleural lobes, nearly flat in their inner half, become convex in their outer portion. Longitudinally the pygidium slopes gently rearward.

Maurice formation; (loc. 151k) Lebarge Creek, near Viola, Uinta County, Wyoming.

*Holotype*.—U.S.N.M. No. 108758a; paratype, No. 108758b.

**MARYVILLIA UTAHENSIS, new species**

PLATE 12, FIGURES 27-32

Oolitic and soft granular limestone beds of the Weeks formation have yielded species of *Maryvillia*. *M. utahensis* is represented by

fairly good material which includes all the various parts. In the striation and structure of the brim, the larger size of the eye, and the wider border of the pygidium, this species approaches *Coosia*. However, it seems better to place the species on the *Maryvillia* side of the boundary and recognize these discrepancies.

The glabella tapers to a rounded front, and in exfoliated specimens is clearly outlined by a deep dorsal furrow. The fixigenes, convex in cross section, are a little less than half the glabellar width. Rather heavy eye lines are accentuated in appearance by the abrupt slope adjacent to them. The width of the brim is equal to half the length of the glabella exclusive of the occipital ring. The rim is demarcated by a change in slope. Heavy striations occur on the front edge of the rim. Eyes rather large, being nearly as long as the brim is wide.

The librigena shows that the suture is intramarginal for a short distance. Its rather wide and strongly striated rim increases in width slightly from the front to the rounded genal angle. The ocular platform is very narrow opposite the anterior portion of the eye. At its widest point, at the rear of the eye, it is not much broader than the rim. The associated hypostoma is nearly circular in outline with the central convex portion occupying less than half of its area. The outer upturned flange is striated in a manner similar to that of the rims on the cranidium and librigena.

The associated pygidium is strongly convex in lateral direction and slopes very steeply longitudinally. The axis, occupying only a little more than half the length of the tail, is not strongly differentiated from the pleural lobes, although it stands completely above them. Axial rings and the anterior pleura are faintly indicated.

Weeks formation; (loc. 32w) Fandango Spring Canyon, Dugway Range, Utah.

*Holotype*.—U.S.N.M. No. 108759a; paratypes, Nos. 108759b-e.

#### MARYVILLIA MARJUMENSIS, new species

PLATE 12, FIGURES 33-35

This species is well represented, and on several pieces of rock cranidia and pygidia lie close together. One fairly large cranidium is figured, but even larger ones are present in the collection. *M. marjumensis* is fully typical of *Maryvillia* in that the pygidial axis extends nearly the full length of the pygidium. As usual the glabella tapers to a rounded front and in exfoliated specimens is clearly defined by a rather deep dorsal furrow, which on the outer test is shallow. Fixigenes average just about half the glabellar width. Eyes are of normal



size. The brim width equals about half the length of the glabella, including the occipital ring. It is gently concave with a rather wide rim indicated by a slight change in curvature. The cranidium is slightly convex in both directions.

The associated hypostoma is almost circular in outline, and is striated on the wide flange which surrounds the convex but depressed central elevation.

The plump pygidium with an axis extending nearly the full length terminates in a postaxial ridge.

Weeks formation; (loc. 30i) 5 miles south of Marjum Pass, House Range, Utah.

*Holotype*.—U.S.N.M. No. 108760a; paratypes, Nos. 108760b-c.

#### MARYVILLIA LOPERI, new species

PLATE 12, FIGURES 36-38

This species is found at two localities in arkosic, calcareous, and quartzitic sandstone. It averages rather large in size compared to other western species. The glabella tapers forward to the rounded front in the usual manner, and is a little longer than in the other species here described. At the eyes the fixigenae are slightly more than half the glabellar width. The eyes are normal in size and position. The brim width is about one-third the glabellar length. A shallow anterior furrow separates a slightly thickened rim. In cross section the cranidium is moderately and evenly convex, but longitudinally it is rather flat.

The associated pygidium is likewise rather convex in cross section, but longitudinally proportionately has greater convexity than the cranidium. The prominent axis occupies nearly three-fourths the length of the pygidium. In exfoliated specimens three pleural grooves are visible on each side.

Sawatch formation; (loc. 6a) Taylor Peak, 4 miles south of Ashcroft; (loc. 6) Italian Mountain, 15 miles northeast of Crested Butte, Colorado.

*Holotype*.—U.S.N.M. No. 108761a; paratype, No. 108761b.

#### MARYVILLIA ALBERTA, new species

PLATE 13, FIGURES 1-4

This species is founded on a single exfoliated cranidium, and a pygidium from a nearby locality is referred to it. The cranidium, typical in all respects, has a large glabella that tapers to a rounded frontal outline. Exfoliated specimens have a strongly developed keel.

At the eyes the fixigenes are half the width of the glabella. The width of the simple, gently concave brim is a little less than the glabellar length. The eyes are slightly larger than usual. In both directions the convexity of the cranidium amounts to little.

The pygidium from a nearby locality, assigned to the species, has a prominent axis which tapers somewhat more than usual. The rear border occupies about one-third the pygidial length, which with the rather large eye, indicates the approach to *Coosia*.

Sullivan formation; (locs. 64i, 64c) Glacier Lake Canyon Valley, 48 miles northwest of Lake Louise, Alberta.

*Holotype*.—U.S.N.M. No. 108762; paratype, No. 108770.

### MARYVILLIA MONTIS, new species

#### PLATE 13, FIGURES 11-13

Several cranidia and pygidia are in hand. The glabella which tapers to a rounded front, is almost without trace of furrows but does have a faint keel. In this species the brim is rather wide, equaling one-third the cranidial length. A slightly thickened rim, separated by a wide anterior furrow, can be seen when the specimen is lighted from the front, but when the direction of lighting is changed the brim appears to be concave without a rim. At the eye the fixigenes are about half the glabellar width. Longitudinally the cranidium is nearly flat. However, the glabella is gently convex and the preglabellar area depressed, while the brim rises until its anterior half extends above the level of the glabella. In cross section there is little convexity.

The prominent pygidial axis occupies three-fourths the length of the pygidium and has a postaxial ridge that reaches practically to the rear margin. Axial and pleural furrows shallow. Moderate convexity is developed in both directions.

Deadwood formation; (loc. 17L)  $\frac{1}{2}$  mile west of Deadwood, Black Hills, South Dakota.

*Holotype*.—U.S.N.M. No. 108763a; paratype, No. 108763b.

### MARYVILLIA HYBRIDA, new species

#### PLATE 13, FIGURES 14-17

Although this species is not fully typical of the genus, the cranidial and pygidial characters appear to be closer to *Maryvillia* than to any other described genus. Therefore *M. hybrida* is placed in this genus for the present. The exfoliated cranidium has a glabella that tapers to a rounded front. The occipital ring is narrow. No trace of glabellar furrows remains. The brim width equals nearly one-third the

glabellar length. It is concave without differentiation of a rim either by furrow or change in contour.

At the eyes the fixigenes are about half the glabellar width, increasing posteriorly to expand in rather large posterolateral limbs. In cross section the cranidium is rather convex with an even curvature, while longitudinally the convexity is greater. The pygidium has a conspicuous axis rising above the pleural lobes. Axial and pleural furrows obliterated. In cross section the profile is rather flat, but longitudinally the axis is convex and the rear portion of the pygidium slopes down steeply.

Cap Mountain formation; (loc. 14d) Bartlett Hollow, Burnet County, Texas.

*Holotype*.—U.S.N.M. No. 108765a; paratype, No. 108765b.

#### MARYVILLIA MOOSENSIS, new species

PLATE 14, FIGURES 15-17

This species is represented by several examples of cranidia and pygidia from a single boulder found in the Moose River, and therefore the association of head and tail is certain. This is the first identification of the genus in the lower beds of the Lynx formation in the Robson District. The matrix is a dark crystalline limestone containing vaughnite pebbles.

The illustrated cranidium is partially exfoliated, and therefore has a deep dorsal furrow and faint glabellar furrows. The slightly thickened rim is a little wider than the preglabellar area. Fixigenes are narrow, averaging about half the glabellar width at its anterior end. An exfoliated pygidium is illustrated, showing the nodes in the axial furrows, and also shallow pleural furrows. The axis tapers very little and slopes down in the rear rather steeply.

Lynx formation (Sullivan equivalent); (loc. 61r) drift in Moose River, 10 miles northeast of Robson Pass, British Columbia.

*Holotype*.—U.S.N.M. No. 108771a; paratype No. 108771b.

#### METEORASPIS Resser, 1935

#### METEORASPIS BANFFENSIS, new species

PLATE 13, FIGURES 5-10

*Meteoraspis* is not yet well understood. Reference of these cranidia and possibly the pygidium to the genus is warranted according to our present knowledge.

The large tumid glabella occupies about three-fourths of the cranidial area. Furrows are only faintly indicated even on the exfoliated cranidium. Occipital furrow and ring are well developed. Brim width

about one-fourth the glabellar length. Thickened rim wider than the nearly flat preglabellar area. Fixigenes narrower than the rim, convex adjacent to the eye. The small, strongly bowed eyes are set parallel to the dorsal furrow. Suture diverges normally anterior to the eye. Relief of the cranidium is considerable as shown in the illustrations. Anterior angles and posterolateral limbs are moderately depressed. Surface closely granulose.

The associated pygidium is similar to certain forms assigned to *Maryvillia* or *Coosella*. Its axis extends about three-fourths the pygidial length. Pleural furrows weakly developed. A rather wide, flat, border is underlain by a striated doublure.

Sullivan formation; (loc. 66m)  $4\frac{3}{4}$  miles northwest of Banff, Sawback Range, Alberta.

*Holotype*.—U.S.N.M. No. 108764a; paratypes, Nos. 108764b, c.

**COOSIA Walcott, 1911**

**COOSIA CANADENSIS, new species**

PLATE 13, FIGURES 18-20

Several pygidia and one cranidium have been segregated. It is a rather small species for the genus but typical in most other respects. The glabella, tapering to a rounded front, is without furrows. The concave brim width is about one-third the glabellar length. A flat rim demarcated by a shallow anterior furrow about equals the preglabellar area in width. Fixigenes narrow, their width being less than one-fourth the glabellar width at both ends of the eye lobe. The fixigenes rise from the dorsal furrow, but the palpebral lobes have a nearly horizontal position. Laterally the glabella is slightly convex, and longitudinally the cranidium attains moderate convexity by depression of the brim and the steepness of the slope in the anterior part of the glabella. The pygidium has a prominent axis occupying a little more than half its length. In dorsal view a postaxial ridge makes the axis appear much longer than it is. Axial rings are faintly shown, but the pleural furrows and grooves are so completely fused that only the anterior pair remains.

Sullivan formation; (loc. 64i) Glacier Lake Canyon Valley, 48 miles northwest of Lake Louise, Alberta.

*Holotype*.—U.S.N.M. No. 108766a; paratype, No. 108766b.

**COOSIA ALBERTENSIS, new species**

PLATE 13, FIGURES 25-28

Although apparently an abundant species, only a few specimens have been segregated in the collection. This is not a large species,

but is typical of the genus. The glabella tapers to a rounded front. A keel is clearly defined and faint shadows indicate glabellar furrows. Brim, one-third the length of the glabella, has a more clearly defined rim than usual. The fixigenes are narrow and the palpebral lobes rather large.

In the pygidium the axis, with fairly deep furrows, occupies about half the pygidial length. The pleural lobes slope down rather gently to the wide border which assumes a horizontal position.

Sullivan formation; (loc. 65i) Glacier Lake Canyon Valley, 48 miles northwest of Lake Louise, Alberta.

*Holotype*.—U.S.N.M. No. 108768a; paratype, No. 108768b.

#### COOSIA DAKOTENSIS, new species

PLATE 13, FIGURES 29-31

Although this large species is abundantly represented, only a few unbroken examples of each part have been freed from the matrix. It occurs in thin limestone lenses composed chiefly of trilobite fragments. Some of the fragments show the heavy doublure characteristic of the genus.

The cranium is fully typical of *Coosia* in its tapering unfurrowed glabella, wide concave brim, and narrow fixigenes. The brim width is considerably more than half the glabellar length. It is without an anterior furrow, but the heavy doublure causes a thickening in the anterior portion. Fixigenes and eyes are normal in development.

Libragene large, with an elongate ocular platform and a heavy rim that extends into a long, heavy, nearly straight genal spine. Brim on both the cranium and libragene striated.

Pygidium normal, with the axis occupying about half the pygidial length. Axial rings well defined, and on exfoliated specimens the pleural furrows are visible.

Deadwood formation; (loc. 17j) Galena, Black Hills, South Dakota.

*Holotype*.—U.S.N.M. No. 108769a; paratypes, Nos. 108769b, c.

#### COOSIA TRIDENTENSIS, new species

PLATE 15, FIGURES 12-17

This species is abundantly represented in the small collection from this locality. Unfortunately the rock is shattered with injection of calcite veins, which with the crowding of the fossils accounts for the difficulty in getting complete specimens.

The glabella tapers rather rapidly to a rounded front. Lighted from certain directions it appears to be sharply truncate because of the contour of the anterior lobe. Another peculiar feature is the



outward curvature of the dorsal furrow slightly anterior of the mid-point of the eye, which creates a small side lobe on the glabella. The concave brim is a little more than one-third the glabellar length. A sudden increase of curvature develops a broad, shallow anterior furrow near the middle of the brim. Between the eyes, with their broad bands, the fixigenes are confined to the palpebral lobes, which are not as wide as the eye band. Anterior to the eye the facial suture diverges rapidly, developing large anterior angles. Since the eyes extend almost to the occipital furrow, there is almost no fixigene behind the eye, and the posterolateral limbs are therefore very narrow.

The pygidium has the typical oval shape, with a tapering axis that occupies about two-thirds its length. A light postaxial ridge is traceable to the margin. Longitudinally the axis is slightly convex, dropping to the nearly flat border with a smooth concave curve. Furrows, weak on the axis, become clearly defined on the pleural lobes when the test is exfoliated.

Pilgrim formation; (loc. 20y) 3 miles north of Trident, north of Logan, Montana.

*Holotype*.—U.S.N.M. No. 108786a; paratypes, Nos. 108786b-g.

COOSELLA Lochman, 1936

COOSELLA TEXANA, new species

PLATE 13, FIGURES 21-24; PLATE 14, FIGURES 2-5

The first species of *Coosella*, typical in all respects, to be recognized in Texas occurs at two localities. Only the holotype cranidium and the nearly complete pygidium were collected at one locality, but several of each of the parts occur at the other place.

The large glabella tapers rapidly to the rounded front. Faint broad depressions shadow the glabellar furrows. The brim width equals a little less than one-third the glabellar length. In cross light the brim is simple and concave, but when the lighting is from the front a broad, slightly thickened rim is demarcated by a shallow anterior furrow. The diagonal set of the eyes and the nondivergence of the anterior facial suture cause the brim to be much shorter than the rear of the cranidium, producing the pinched effect in the anterior part of the cranidium characteristic of the genus. At the anterior end of the eye lobe the fixigene equals half the glabellar width at the same point, while at the rear of the eye lobe the same relationship is less than one-third. This shows that the fixigene retains its width but little changed, whereas the glabella expands rapidly. The eyes are of normal size, situated opposite the anterior portion of the glabella, and are set parallel to the dorsal furrow.

The axis is about half as long as the pygidium and although it rises above the pleural lobes, its convexity is not great. On the exfoliated portion axial furrows and the pleural grooves are clearly indicated by shallow furrows.

Cap Mountain formation; (loc. 14d) Bartlett Hollow, and (loc. 67a) Potatotop, 7 miles northwest of Burnet, Texas.

*Holotype*.—U.S.N.M. No. 108767a; paratypes, Nos. 108767b, 108773a, b.

**COOSELLA BREVIS**, new species

PLATE 14, FIGURES 6-9

Only the illustrated incomplete cranium and pygidium have been found in this small collection. This species is fully characteristic of *Coosella* in features of both the head and tail. The glabella, which tapers to a rounded front, lacks glabellar furrows. On the other hand the occipital furrow and ring are clearly defined. At the anterior end of the eye the fixigene is about half the glabellar width. The fixigene maintains the same width with little change. Owing to the moderate divergence of the anterior facial suture, there is a slight expansion in front of the eye. The brim width equals nearly half the glabellar length. It has a heavily striated swollen rim, defined by the anterior furrow. The preglabellar area, which is wider than the rim, is depressed below both the rim and glabella.

The eye lobes, about half as long as the glabella, are not greatly bowed and are set nearly parallel to the converging dorsal furrow.

The almost semicircular pygidium is slightly wider than long. The axis stands above the pleural platforms, and extends back for more than two-thirds the pygidial length. It slopes sharply downward near the posterior end to a slight postaxial ridge. Axial and pleural furrows are shallow, but clearly defined in the exfoliated type. Since the test is thick it is probable they are not to be seen on the outer surface. The doublure has a width equal to about one-fourth the pygidial length.

Warrior limestone; (loc. 38e) 1 mile northwest of Benore, and 5 miles west of State College, Pennsylvania.

*Holotype*.—U.S.N.M. No. 108774a; paratype, No. 108774b.

**PTEROCEPHALINA** Resser, 1938

**PTEROCEPHALINA TEXANA**, new species

PLATE 14, FIGURES 32, 33

Only the holotype pygidium has been found in this collection. The wide axis with at least four rings tapers to a rather sharp point, back

of which a postaxial ridge extends to the indented median margin. The pleural platforms are shaped as small triangles, considerably curved to meet the wide concave border. This border develops sizeable flanges at the posterior angles, giving the rear a rather straight margin and the entire pygidium a quadrate shape.

Wilberns formation; (loc. 69) Honey Creek, 8 miles southeast of Llano, Texas.

*Holotype*.—U.S.N.M. No. 108780.

#### PTEROCEPHALINA NOTHA, new species

##### PLATE 14, FIGURES 34-38

The pygidium is typical of the genus. The associated cranidium assigned to the species differs from the head supposed to represent *P. bilobata*, but is like those assigned to the other species of the genus.

The glabella which has two pairs of short furrows, tapers to a poorly defined front, as shown in the side views. This characteristic is due not only to the shallowness of the anterior dorsal furrow but also to the fact that the preglabellar area and the anterior fourth of the glabella form a slope of uniform curvature to the depths of the concavity in the brim. The wide brim rises sharply and the outer portion of the rim is somewhat thickened. A slight change in slope marks the inner edge of the rim which in itself is very concave. Since it is so poorly marked, light must strike this angle properly in order to make it visible. It will be noted that the rim is scarcely perceptible in the dorsal view and in one of the side views. The fixigenae rise rather steeply to the palpebral lobes, on which a strongly curved eye occupies a prominent position because it has a wide swollen eye band. Preglabellar area and part of rim marked by vertical anastomosing lines. In the pygidium the axis is long and rather slender, a postaxial ridge connecting it with the indented median margin. A wide border is produced by the concave portion underlain by the doublure.

Mendha limestone; (loc. 7j) 1 mile north of Italian Ranch foothills, north end of Quinn Canyon Range, Nevada.

*Holotype*.—U.S.N.M. No. 108781a; paratypes, Nos. 108781b-d.

#### PTEROCEPHALINA BILOBATA (Hall and Whitfield)

##### PLATE 14, FIGURES 39-43

*Dicelloccephalus* (*Pteroccephalus*) *bilobatus* HALL and WHITFIELD, U. S. Geol. Expl. 40th Par. vol. 4, p. 226, pl. 2, fig. 36, 1877.

*Dicelloccephalus bilobatus* WALCOTT, U. S. Geol. Surv. Monogr. 8, p. 40, 1884.

*Platycolpus bilobatus* WALCOTT, Smithsonian Misc. Coll., vol. 57, No. 13, p. 349, 1914.

*Pterocephalina bilobata* RESSER, *ibid.*, vol. 97, No. 10, p. 42, 1938.

Additional specimens of this species are figured in order that it may be better understood. A small tail is figured to show the features at that stage. The large cranidium, from which a rim of unknown but evidently considerable width has been broken away, is tentatively assigned to the species.

Secret Canyon shale; (loc. 65) east side of Sierra Canyon, opposite Pinnacle Peak; and (loc. 61) south of Hamburg Mine, Eureka District, Nevada.

*Holotype*.—U.S.N.M. No. 24568; plesiotypes, Nos. 108782a-c.

#### PTEROCEPHALINA POGONIPENSIS, new species

PLATE 15, FIGURES 1-2

Several small pieces of very fossiliferous limestone contain a pygidium and a cranidium regarded as belonging to the same species. Originally it was identified as *P. flabellifer*.

The cranidium is small for the genus. The glabella occupies more than half the cranidial length and since it is exfoliated, three pairs of recurved furrows are faintly visible in cross light. The concave brim is divided into a slightly convex preglabellar area and a wider, flat, somewhat upturned rim. The convex fixigenae are less than half the glabellar width.

As may be observed in the illustrations the axis occupies nearly the full length of the pygidium. It is almost straight on top, sloping back at an even rate to the short postaxial ridge. Axial and pleural furrows are well developed, the latter extending to the margins. Though the lateral margins are somewhat extended, the border is less flared than in more typical species.

Secret Canyon shale; west side of Pogonip Mountain, White Pine District, Nevada.

*Holotype*.—U.S.N.M. No. 108783a; paratype, No. 108783b.

#### PTEROCEPHALINA GRATA, new species

PLATE 15, FIGURES 3-6

This small distinctive species is represented by several cranidia and pygidia. The narrow cranidium has a large slightly tapered glabella and a concave brim about one-third as wide as the glabellar length. The demarcation of a wide rim is so faint that only in a certain light does the brim appear to be anything but a simple concave plate.

The axis occupies only about half the pygidial length. It is slightly concave in a longitudinal direction and slopes abruptly to the wide border. Furrows are visible on the axis and in the anterior portions of the pleural platforms. A slight postaxial ridge extends to the rear margin.

Secret Canyon shale; (loc. 23b) ridge east of Hamburg Ridge, Eureka District, Nevada.

*Holotype*.—U.S.N.M. No. 108784a; paratype, No. 108784b.

#### PTEROCEPHALINA UTAHENSIS, new species

PLATE 15, FIGURES 7-11

A very fine species of *Pteroccephalina* has been found in western Utah. This genus should be represented in other formations of the same age throughout the cordilleran region.

The glabella tapers to a truncated front, where the dorsal furrow is almost obliterated. Three pairs of glabellar furrows are faintly defined, the posterior pair having a very irregular course. The wide, gently concave brim occupies nearly half the glabellar length. Fixigenes are narrow, being only one-third the glabellar width between the eyes and the dorsal furrow. Eye bands are heavy. Anterior to the eyes the facial suture diverges moderately to meet the wide brim. The axis occupies less than half the length of the pygidium and stands above the small pleural platforms. Three rings are clearly defined. Three pleural furrows, decreasing in depth from posteriorly, are visible. The wide border is nearly flat, and has a wide medial indentation.

Orr formation; (loc. 33d) east side of Fish Spring Range, Utah.

*Holotype*.—U.S.N.M. No. 108785a; paratype, No. 108785b.

#### BURNETIDAE, new family

Kobayashi established the Dokimocephalinae as a subfamily in the Solenopleuridae Angelin, to include the genera *Burnetia*, *Dokimocephalus*, *Iddingsia*, *Elkia*, and *Acrocephalites*. The last-named genus superficially resembles the others, but since it is a Middle Cambrian Atlantic Province genus and therefore far removed from the others in time and space, its relationship may be questioned. In my opinion *Acrocephalites* is related to *Solenopleura* and should remain in that family. The Burnetidae are not from the *Solenopleura* line but have descended from trilobites found in the cordilleran region. To the named genera must be added *Berkeia*, and several others still undescribed.



Thus constituted, the new family is found to play a rather prominent role in the Upper Cambrian, beginning in *Crepicephalus* time and extending to about the middle of the Upper Cambrian. Wide variation appears to exist between the ordinary swollen rim of *Berkeia* and the enormous snout of *Dokimocephalus*. However, since the glabella, fixigenes, eyes, and furrows are much alike in these genera, the variations in rim shape are not to be looked upon as a separating but rather as a uniting feature of the family. Variability of the rim is found between species of the same genus. Consequently, with such a characteristic, wide variation must be expected in the family, and as such becomes a family characteristic.

BURNETIA Walcott, 1924

BURNETIA INTERMEDIA, new species

PLATE 17, FIGURES 10, 11

*B. intermedia* is one of the linguloid forms. Its glabella tapers moderately to a rounded front. Two pairs of glabellar furrows are clearly defined. The enlarged neck ring extends into a long, erect spine. At the anterior end of the eyes the fixigenes are less than one-third the glabellar width. The palpebral lobes are sharply angulated. The palpebral furrow is wide and eye band heavy. The brim attains a width equal to the length of the glabella exclusive of the neck ring, and the preglabellar area is less than one-fifth this width. Viewed from the rear the glabella is roundly convex and the fixigenes rise to the eyes. Viewed from the front, however, the relative convexity of the several parts is much less, though the anterior fixigenes drop steeply to the depressed anterior angles. Greater convexity of the cranium is found in the longitudinal profile, attained by a rather even curvature of both glabella and brim, which together form a smooth sigmoid curve. Surface granulose.

Honey Creek limestone; (loc. 12p) 4 miles southeast of Hemmepin, Arbuckle Mountains, Oklahoma.

*Holotype*.—U.S.N.M. No. 108805.

BURNETIA ALTA, new species

PLATE 17, FIGURES 12-14

The long glabella has two pairs of furrows. In dorsal view it appears to be narrow and tapered more rapidly than in most species. If, however, the excessive convexity in both directions is taken into consideration the area of the glabella is really large. The brim is not wide, being less than half the glabellar length exclusive of the neck

ring. The preglabellar area is less than one-fourth the rim width. Longitudinally the convexity of the cranidium is so great that the front fourth has taken the position of a  $90^\circ$  angle with the posterior portion of the glabella. From that position the brim takes a less steep angle and is in itself nearly flat. In cross section the glabella is also very convex, attaining a height equal to about one-third its length. Because the anterior angles are also greatly depressed this species becomes one of the most convex Cambrian trilobites.

The associated librigenae is large. The wide and long ocular platform is only slightly convex and lacks a furrow. Toward the long genal spine the librigenae becomes convex forming a ridge that extends into the genal spine. Elevated portions of surface of head and cheek coarsely granulated.

Davis formation; (loc. 11k) Federal Lead Mine No. 4, Flat River, Missouri.

*Holotype*.—U.S.N.M. No. 108801a; paratype, No. 108801b.

#### **BURNETIA EXTENSA**, new species

PLATE 17, FIGURES 15-22

This species is abundantly represented by numerous cranidia, several librigenes, and possibly also by a pygidium. It is the extreme of the linguloid forms thus far found. It will be observed that a slight variation has been allowed among the specimens figured.

The glabella, rounded in front, has two pairs of furrows. The occipital furrow is almost interrupted at the center, and the neck ring carries a large spine. The brim, which comes to a rather sharp point, exceeds the length of the glabella exclusive of the neck ring. A narrow preglabellar area is present. Eyes are strongly bowed and have heavy eye bands. The librigenes illustrated show that the suture is intramarginal for a considerable distance and that the wide doublure apparently extends all the way across, with an increase in width toward the middle. The associated pygidium has a long, stout axis and pleural lobes that are slightly convex, sloping to a concave border.

Honey Creek limestone; (loc. 89v) West Timbered Hills, Arbuckle Mountains, Oklahoma.

*Holotype*.—U.S.N.M. No. 108807a; paratypes, Nos. 108807b-g.

#### **BURNETIA EXILIS**, new species

PLATE 17, FIGURES 23-27

This species also is well represented by cranidia. Because of its nearly circular anterior outline it is closer to the normal form. In

fact, taken as a whole, the cranidium gives the impression of circularity. At the same time *B. exilis* is a convex form, the glabella standing high above the fixigenes and the brim continuing the downward slope of the anterior portion of the glabella. Eyes, fixigenes, glabellar furrows, and eye bands are similar to corresponding parts in species of average structure for *Burnetia*. The brim width is about three-fourths the glabellar length and has only a narrow preglabellar area. Viewed from the front, the brim has an even curvature between the depressed anterior angles. In cross light several shallow secondary furrows parallel to the front margin are visible, but they may represent double impressions. Surface of elevated portions granulated.

Honey Creek limestone; (loc. 89v) West Timbered Hills, Arbuckle Mountains, Oklahoma.

*Holotype*.—U.S.N.M. No. 108808a; paratypes, Nos. 108808b, c.

#### BURNETIA ECTYPA, new species

PLATE 17, FIGURES 30, 31

Only a small fragment in addition to the beautiful holotype cranidium has been found. The glabella, well rounded in front, has the rear pair of glabellar furrows of normal development and very shallow indentations indicating the second pair. No nuchal spine and practically no preglabellar area remain. The brim is about two-thirds the length of the glabella including the neck ring. Longitudinally the glabella is rather highly and evenly convex. The concave brim is set at such an angle that it makes the cranidium as a whole high. In cross section the glabella rises steeply above the dorsal furrow to a somewhat angulated median portion. The rim is evenly convex between the moderately depressed anterior angles.

Honey Creek limestone; (loc. 89v) West Timbered Hills, Arbuckle Mountains, Oklahoma.

*Holotype*.—U.S.N.M. No. 108809.

#### BURNETIA LINGULA, new species

PLATE 17, FIGURES 32, 33

A single cranidium of another linguloid form, much like *B. extensa*, has greater convexity and a brim of the same width as the glabellar length. A narrow preglabellar area remains. Viewed from the side the glabella is gently convex at the rear, increasing its rate of curvature until the anterior third is turned sharply downward. The proclivity of the glabella is continued by the brim at a decreasing rate for nearly half its width, beyond which point the rate of slope de-

creases until the anterior part is nearly horizontal. In cross section the glabella is moderately convex, the anterior angles not greatly depressed and the anterior portion of the rim nearly flat. Surface not preserved.

Honey Creek limestone; (loc. 89v) West Timbered Hills, Arbuckle Mountains, Oklahoma.

*Holotype*.—U.S.N.M. No. 108810.

**BURNETIA CURTA, new species**

PLATE 17, FIGURES 28, 29

A cranidium has a peculiar large glabella with a nearly circular front outline. Three pairs of furrows are visible. Fixigenes and eyes are normal. The brim width is not much more than half the glabellar length and has a narrow preglabellar area. The neck ring extends into a long elevated spine that nearly equals the length of the cranidium. Convexity is not great in cross section, but longitudinally it is considerably more.

Honey Creek limestone; (loc. 9q) Blue Creek Canyon, Wichita Mountains, Oklahoma.

*Holotype*.—U.S.N.M. No. 108811.

**BURNETIA CAVA, new species**

PLATE 20, FIGURES 1-3

A cranidium and associated librigena impression represent this species. Glabella normal in size and shape although it possibly is a little wider than average. Two pairs of furrows are well developed and a third is faintly indicated. The neck ring may have borne a spine, but if so, it was no more than a node. The brim width is considerably greater than half the glabellar length. Most of it consists of a concave rim with only a narrow preglabellar area demarcated by a shallow furrow. Fixigenes average only a little more than a fourth of the glabellar width, and the divergence of the suture anterior to the eye produces large anterior angles into which the wide rim extends. The sharply bowed eyes are set at a somewhat more divergent angle than the dorsal furrow and are situated slightly in advance of the occipital furrow, leaving a considerable posterolateral limb. The broad fixigene assigned to the species has a rather large genal spine. The suture evidently is intramarginal to the center, but since it is broken away in front, that structure is not readily observable.

Surface covered with evenly spaced granules except in furrows. They are arranged in radiating lines on the librigena.

Ore Hill formation; (loc. 107v)  $\frac{1}{2}$  mile northwest of Drab, Pennsylvania.

*Holotype*.—U.S.N.M. No. 108827a; paratype, No. 108827b.

**BURNETIA EDWARDSI**, new species

PLATE 20, FIGURES 20, 21

A large cranidium associated with species of *Taenicephalus* and *Orygmaspis* occurs on a hand specimen of soft sandstone. Although the brim is narrow, the entire structure is typical of the genus. The glabella, tapering at a normal rate, has several sets of broad, shallow furrows faintly indicated. The occipital furrow also is broad and shallow. The concave brim is subdivided almost equally between a rim and a preglabellar area. Its width is just a little more than a fourth of the cranidial length. The fixigenes are a little less than half the glabellar width. The sharply bowed eyes are of normal size but situated a little farther forward than the ordinary position for the genus. In front of the eyes the sutures diverge considerably to form large anterior angles. Longitudinally the head forms a sigmoid curve with the rear part of the glabella nearly horizontal and the anterior part arched down sharply to the concave brim. Viewed laterally the glabella stands completely above the fixigenes and has a fairly even curvature.

Franconia sandstone; 2 miles west of Clifton, Monroe County, Wisconsin.

*Holotype*.—U.S.N.M. No. 108832.

**BURNETIA PENNSYLVANICA**, new species

PLATE 21, FIGURES 29-31

Several cranidia and a librigena from the type locality have been assigned to this species. From the other locality there are other less complete cranidia and fragments of other parts. This species is typical of the genus, belonging to the group in which the brim is not expanded. Restoration of the front of the glabella from the counterpart allows the cranidium to be reproduced in its entirety. The glabella tapers forward at the usual rate for cranidia of this type. The rear pair of furrows is deeply impressed, while pits next to the dorsal furrow indicate the position of the other two pairs. The width of the moderately concave brim is just half the glabellar length exclusive of the occipital ring. The rim is much wider than the preglabellar area and is not evenly concave because it has a furrowlike depression paralleling the anterior furrow. The eyes of normal size are so sharply bowed that the palpebral lobe is angulated. At the anterior



end of the eye the fixigene is less than a third the glabellar width. Anterior angles and narrow posterolateral limbs are strongly depressed. Surface of exterior granulose, evidently with two sets of granules. Exfoliated surfaces are even more closely covered with coarser granules varying considerably in size.

Ore Hill formation; (loc. 107e) 1 mile south of Ore Hill; and (loc. 107v)  $\frac{1}{2}$  mile west of Drab, Pennsylvania.

*Holotype*.—U.S.N.M. No. 108842a; paratype, No. 108842b.

IDDINGSIA Walcott, 1924

IDDINGSIA NEVADENSIS, new species

PLATE 16, FIGURES 15-17

A cranidium and librigenae which were previously identified as *I. robusta*, differ from that species in several respects. *I. nevadensis* is characterized by the usual large glabella on which the rear pair of furrows are deep and the next pair short and shallow. A wide occipital furrow separates a prominent neck ring. At the anterior end of the eye the fixigenes are about one-third the glabellar width. In width the brim is just half the length of the glabella including the neck ring. It is divided about equally into a somewhat convex preglabellar area and a slightly thickened rim. Longitudinally the cranidium is convex, the glabella having a nearly even curvature except toward the front, where there is a slight decrease. On the other hand the brim as a whole is moderately concave. In cross section the glabella is convex, and the librigenes rise from the dorsal furrow rather steeply. The anterior angles are sharply depressed. Likewise the posterolateral limbs appear to have been considerably depressed. The associated librigenae has a large ocular platform and a rim to match the brim width. A heavy genal spine of unknown length is built from the heavy rim and the thickened rear portion of the cheek.

This species differs from *I. robusta* in its longer glabella and relatively narrower rim. In *I. robusta* the brim as a whole continues the downward slope of the anterior half of the glabella, thus giving the cranidium much greater convexity.

Secret Canyon shale; (loc. 61) South of Hamburg Mine, Eureka District, Nevada.

*Holotype*.—U.S.N.M. No. 108796a; paratype, No. 108796b.

IDDINGSIA UTAHENSIS, new species

PLATE 16, FIGURES 18-20

Several cranidia from the Dugway Range are the basis for a species, which in general appearance resembles *I. nevadensis*. *I. utahensis* is

characterized by a normal glabella on which two pairs of furrows are clearly impressed. At a point immediately in front of the eye the fixigene is about one-third the glabellar width. Divergence of the facial suture in front of the eye develops moderately large anterior angles. The brim width is about two-thirds the glabellar length including the occipital ring. The slightly convex preglabellar area is about two-thirds the width of the rim. Little curvature exists in the rear half of the glabella, but the forward part turns down sharply. The preglabellar area continues that slope, but the rim is turned toward a horizontal position. Surface granulose, as usual.

Orr formation; (loc. 32t) Fandango Spring Canyon, Dugway Range, Utah.

*Holotype*.—U.S.N.M. No. 108797a; *paratype*, No. 108797b.

#### IDDINGSIA MISSOURIENSIS, new species

PLATE 16, FIGURES 21-26

This is a rather prolific species, associated with *Berkeia*, *Pteroccephalia*, and other genera. Besides the numerous cranidia several librigenes also represent the species. The glabella, tapering to a somewhat truncated front, has three pairs of well-developed furrows. The width of the flaring brim equals about two-thirds of the glabellar length. In the middle the flat rim is wider than the preglabellar area. The slightly convex preglabellar area continues the downward slope of the anterior portion of the glabella, but the nearly flat rim has a less steep slope. At the anterior end of the eye the fixigene is one-third as wide as the glabella. It rises sharply from the dorsal furrow but is in itself not very convex. The strongly bowed eyes are situated far back, practically in contact with the occipital furrow. An eye line extends forward from the eye to the anterior glabellar lobe. Longitudinally the cranidium is strongly convex, the relief being attained by a slight curvature of the posterior half of the glabella and a strong down-curving of the anterior half, continued by the slope of the brim. Laterally the glabella rises little above the level of the palpebral lobes, but the posterolateral limbs are sharply depressed. At the eye lines the fixigenes slope abruptly downward to the anterior angles. A small node occurs on the well-defined occipital ring.

The rather large librigena has a long stout genal spine. At the eye the fixigene rises steeply to the ocular platform which has a globular convexity. The rim is flat and the suture intramarginal at least for half and possibly all the distance to the center. None of the specimens preserves the doublure which probably maintains its width across the

cranium. A peculiar feature of the librigena is the convexity that begins about halfway back in the rim and extends into the round, elevated genal spine.

Davis formation; (loc. 11k) Federal Lead Mine No. 4, Flat River, Missouri.

*Holotype*.—U.S.N.M. No. 108798a; paratypes, Nos. 108798b-d.

#### IDDINGSIA BICINCTA, new species

PLATE 16, FIGURES 27-29

Several plump cranidia from Blue Creek Canyon constitute another species. Compared with others in the region the distinctive feature seems to be the subdivision of the brim into two approximately equal portions. The rather short glabella is rounded in front and rises above the dorsal furrow with an even curvature. Furrows are so faint that they are scarcely traceable. The occipital furrow on the other hand is wide and deep, and the ring carries a long slender spine. The brim width nearly equals the length of the glabella exclusive of the neck ring. At the anterior end of the eye, the fixigenae are only one-third the glabellar width. Divergence of the facial suture forms rather large anterior angles. Longitudinally the cranium is convex, the rear half of the glabella being nearly level and the anterior third sharply curved, and the slightly convex preglabellar area continues its downward trend, while the rim turns to a nearly horizontal position. In cross section the glabella appears elevated with a nearly circular curvature. In like manner the fixigenae near the eyes are also convex. There is but a slight depression of the anterior angles so that the slope of the preglabellar area is not much more at the sides than in the middle. Surface of test nearly smooth. However, the exfoliated preglabellar area is marked by rather strong vertical anastomosing lines.

Honey Creek limestone; (loc. 9q) Blue Creek Canyon, Wichita Mountains, Oklahoma.

*Holotype*.—U.S.N.M. No. 108799.

#### IDDINGSIA CRASSIMARGINATA, new species

PLATE 16, FIGURES 30-32

This cranium, associated with *I. missouriensis*, is very distinct, owing to its wide, flaring brim and relatively small glabella. The glabella tapers to a slightly rounded front and has two pairs of furrows. The brim is nearly as wide as the length of the glabella exclusive of the occipital ring. It has a wide, slightly concave rim

nearly one and one-half times as wide as the preglabellar area. Eyes are strongly bowed and situated just in front of the occipital furrow. At the anterior end of the eye the fixigenes are less than half the glabellar width. In cross section this species has little relief. The glabella rises to a rounded median angle and the fixigenes rise without curvature to the palpebral lobes. Longitudinally the glabella is gently curved, increasing its declivity near the front, while the slightly concave brim slopes less. The anterior angles are moderately depressed, but the elevated palpebral lobes accentuate the steepness of the slopes of the anterior fixigenes immediately forward of the eye lines.

Davis formation; (loc. 11k) Federal Lead Mine No. 4, Flat River, Missouri.

*Holotype*.—U.S.N.M. No. 108800.

#### IDDINGSIA ALPERSENSIS, new species

PLATE 16, FIGURES 33-38

The glabella is rounded in front and practically without furrows. The brim width is about half the length of the glabella including the thickened neck ring, which carries a long spine. Because of the circular anterior outline of the cranidium and the comparatively much less curved anterior furrow, the rim widens appreciably toward the center, where its width is about equal to the preglabellar area. At the anterior end of the eye the fixigene is about one-third the glabellar width. In this species the eyes are not so strongly bowed, nor do they extend back to the occipital furrow. As a whole the cranidium has considerable convexity. In the rear the glabella stands high above the dorsal furrow, but this relationship decreases anteriorly. Thus a forward slope of the whole is created, which is continued by the convex preglabellar area. The wide flat rim rises somewhat above a horizontal position. A slight rise brings the fixigenes up to the palpebral lobes. Anterior angles depressed. Preglabellar area marked by strong anastomosing lines.

Honey Creek limestone; (loc. 12p) 4 miles east of Alpers, Arbuckle Mountains, Oklahoma.

*Holotype*.—U.S.N.M. No. 108801a; paratypes, Nos. 108811b, c.

#### IDDINGSIA (?) QUINNENSIS, new species

PLATE 16, FIGURES 39-41

At first glance this cranidium seems to be far removed from *Iddingsia*. However, when its features are examined individually, each feature fits *Iddingsia* more closely than any other genus. In other

words, while the ensemble does not look so much like *Iddingsia*, the separate features fall readily within its generic limits.

The glabella is large, nearly rectangular, slightly rounded in front, and has three pairs of furrows. The neck ring carries a small spine. Since the anterior facial suture diverges at a small angle and the anterior margin is rather straight, the cranidium as a whole has a quadrangular shape. The brim, divided almost equally between rim and preglabellar area, equals about half the glabellar length exclusive of the neck ring. At the anterior end of the eye the fixigene is less than half the glabellar width. The eyes situated far back against the occipital furrow are rather strongly bowed and have particularly heavy palpebral furrows and eyebands.

Mendha limestone; (loc. 7j) 1 mile northwest of Italian Ranch foothills, Quinn Canyon Range, Nevada.

*Holotype*.—U.S.N.M. No. 108802a; paratype, No. 108802b.

#### IDDINGSIA ANATINA, new species

##### PLATE 17, FIGURES 1, 2

This neat species is characterized by its smooth, rounded glabella. The occipital furrow is narrower than usual, but the neck ring expands in the center and has a long spine. The brim width equals the length of the glabella exclusive of the occipital ring. Owing to the forward projection of the anterior margin, the rim at its center exceeds the width of the preglabellar area. Fixigenes are of average size and shape, being peculiarly marked by the swellings in the inner rear portion of the palpebral lobe. The evenly and sharply bowed eyes have heavy bands. In cross section the evenly convex glabella rises above the dorsal furrow. The fixigenes opposite the eyes are also convex. Longitudinally the glabella is gently convex. The cranidium as a whole slopes forward, its declivity being continued by the preglabellar area as far as the anterior furrow, beyond which the rim is turned up somewhat. Brim covered with vertical anastomosing lines.

Honey Creek limestone; (loc. 9q) Blue Creek Canyon, Wichita Mountains, Oklahoma.

*Holotype*.—U.S.N.M. No. 108803.

#### IDDINGSIA SIMPLICITAS, new species

##### PLATE 17, FIGURES 3-9

This prolific species, represented by many cranidia and several librigenes was first regarded as representing a new genus. However,



upon close examination it appears to be merely a simplification of the regular *Iddingsia* features.

The fairly large glabella has two pairs of faint furrows. The expanded neck ring, separated from the glabella by a strong furrow, carries a large spine in an elevated position. Although in the posterior position of the genus *Iddingsia*, the eyes are sufficiently removed from the occipital furrow to leave a small gap. Measuring along the contours of the brim, its width equals the length of the glabella exclusive of the neck ring. A median boss is developed in the convex preglabellar area, thus accentuating the variant aspect of the species. A change in contour alone marks the position of the anterior furrow. In different light directions this concavity shifts its position, causing the rim to appear relatively wider or narrower than the preglabellar area. The fairly large librigenae has a moderately convex ocular platform. The suture is intramarginal for a considerable distance. A swelling beginning in the rear portion of the rim and the outer corner of the ocular platform, continues into the long genal spine which is in a horizontal position, thus having a considerable upward and outward course from the ocular platform.

Honey Creek limestone; (loc. 89y) West Timbered Hills, Arbuckle Mountains, Oklahoma.

*Holotype*.—U.S.N.M. No. 108804a; paratypes, Nos. 108804b-d.

BERKEIA Resser, 1937

BERKEIA COMES, new species

PLATE 15, FIGURES 18-21

Although several cranidia are available, the pygidium has not been determined.

All of the cranidia are exfoliated, and therefore the furrows appear much deeper than on the exterior of the test. The large glabella is well rounded in front. Because of the enlargement of the dorsal furrow the glabella appears to be restricted posterior to the rear pair of glabellar furrows. Three pairs of recurved furrows are clearly impressed. The swollen occipital ring is elevated and carries a short spine. The brim width is about one-fourth the glabellar length. In dorsal view it appears to be divided almost equally between the preglabellar area and the rim, but in side view the rim seems to be relatively narrower. This subdivision is attained by a change in slope between the somewhat convex preglabellar area and the slightly thickened rim, turned up a little above the horizontal position. Opposite the eyes the fixigenae equal one-third the glabellar width. Owing

to the sharp depression of the anterior angles, the divergence of the anterior facial suture is not apparent. Back of the eyes the postero-lateral limbs, also sharply depressed, are about three times the width of the occipital ring. Laterally the glabella stands completely above the fixigenes with very steep sides. Longitudinally the entire cranium is very convex.

Deadwood formation; (loc. 88a) Deadwood, Black Hills, South Dakota.

*Holotype*.—U.S.N.M. No. 108787a; *paratype*, No. 108787b.

### **BERKEIA SARATOGENSIS, new species**

PLATE 15, FIGURES 22-25

Although this species is not fully typical of the genus in that the rim is narrower than the preglabellar area, the difference in appearance may be due to the fact that on these specimens the test is preserved. However, since this form does not fit in any other existing genus and because its departure from the characteristics of *Berkeia* is confined to the narrowness of rim, the species is placed in that genus.

As usual the large glabella tapers to a rounded front and has three pairs of recurved furrows. The brim width is somewhat less than a third the glabellar length. The preglabellar area is more than twice the width of the slightly upturned rim. Opposite and behind the eye the fixigenes average about half the glabellar width. Divergence of the suture creates fairly large anterior angles. In cross section the total convexity across the eyes is moderate, although both the glabella and fixigenes are individually convex. By depression of the anterior angles and of the posterolateral limbs, both the front and back portions of the cranium attain considerable convexity. Longitudinally the cranium is strongly convex, attained by a rather even curvature throughout.

Potsdam sandstone; Greenfield, northwest of Saratoga, New York.

*Holotype and paratypes*.—New York S. M.; casts U.S.N.M. Nos. 108792a-c.

### **BERKEIA NEVADENSIS, new species**

PLATE 15, FIGURES 26, 27

*B. nevadensis*, represented at several localities, differs from *B. affinis* chiefly in its lesser convexity in longitudinal direction. This difference is not merely a matter of preservation, for *B. nevadensis* is represented by nearly a score of specimens.

Features which make this an average species of the genus include similar glabellar proportions and furrows, narrow convex fixigenes, and brim subdivided into convex preglabellar area and rim of equal width. In dorsal view this species looks like *B. affinis*, but in side view, although nearly equally convex in the glabella, it has a brim less convex in its individual parts and as a whole much less downturned.

Secret Canyon shale; (loc. 61) south of the Hamburg Mine, and (loc. 62) north of Adams Hill, Eureka District, Nevada.

*Holotype*.—U.S.N.M. No. 108788a; paratype, No. 108788b.

#### BERKEIA RETUSA, new species

PLATE 15, FIGURES 28-30

This species acquires a peculiar aspect for two reasons. First, the preglabellar area is wider than the rim, and second, the chief distinction lies in the slight swelling of the middle portion of the preglabellar area. Glabellar furrows are well developed. Eyes and fixigenes are of normal size and shape. As stated, the preglabellar area is wide and convex. Longitudinally the cranidium is rather evenly convex, turning down more rapidly in the anterior half. In cross section the glabella and fixigenes are each convex, but taken together are rather flat in profile. The anterior angles and posterolateral limbs are moderately depressed.

Honey Creek limestone; (loc. 12p) 4 miles southeast of Hennepin, Arbuckle Mountains, Oklahoma.

*Holotype*.—U.S.N.M. No. 108789a; paratype, No. 108789b.

#### BERKEIA WICHITAENSIS, new species

PLATE 15, FIGURES 31-33

The rather long cranidium has the usual large glabella, in which two pairs of furrows are well defined. The fixigenes average less than a third the glabellar width. The preglabellar area is wider than the rim. In this species the rim expands somewhat to the middle, which together with the more angular anterior margin exaggerates the actual length of the cranidium.

The small pygidium, tentatively assigned to the species, has a wide axis occupying more than half its length, and flat pleural lobes. As a whole the pygidium is oval in outline.

Honey Creek limestone; (loc. 91L) Big Baldy, Wichita Mountains, Oklahoma.

*Holotype*.—U.S.N.M. No. 108790a; paratype, No. 108790b.

**BERKEIA ANGUSTATA**, new species

PLATE 15, FIGURES 34-39

*B. angustata* is a prolific species which appears to be narrower than others from the same region. Its aspect is due to the relatively long glabella and the angulation of the anterior margin. The glabella, rounded in front, has two well-developed pairs of furrows. The neck ring extends into a short blunt spine. In this species the preglabellar area is considerably wider than the brim.

Honey Creek limestone; (loc. 89y) West Timbered Hills, Arbuckle Mountains, Oklahoma.

*Holotype*.—U.S.N.M. No. 108791a; paratypes, Nos. 108791b, c.

**BERKEIA SCULPTILIS**, new species

PLATE 16, FIGURES 1-4

This small species is not fully typical of the genus because of the relative depression and constriction of the middle portion of its preglabellar area. The prominent glabella stands well above the fixigenes. It is rounded in front and has three pairs of furrows on exfoliated specimens. The fixigenes average nearly half the glabellar width and the brim width equals about one-third the glabellar length including the neck ring. Both the anterior angles and the posterolateral limbs are sharply downturned so that in dorsal view the strong curve of the brim is exaggerated. The rim is thickened in the center, where it is about as wide as the preglabellar area.

Honey Creek limestone; (loc. 12k) Honey Creek, 7 miles north of Springer, Wichita Mountains, Oklahoma.

*Holotype*.—U.S.N.M. No. 108793a; paratype No. 108793b.

**BERKEIA JUCUNDA**, new species

PLATE 16, FIGURES 5-10

This is the smaller of the two species in the Davis formation. It is typical of the genus in every respect, agreeing rather closely with those Oklahoma species which are characterized by the wide preglabellar area. The moderately convex glabella tapers at the normal rate to a rounded front and has three pairs of furrows on exfoliated specimens. The fixigenes are narrower than the brim, averaging about one-third the glabellar width. The eyes are rather large, and the palpebral lobe is angulated near its center. The brim width equals half the glabellar length exclusive of the neck ring. It has a nearly even brim about half as wide as the preglabellar area. The front margin is slightly angulated in the middle.

Davis formation; (loc. 11k) Federal Lead Mine No. 4, Flat River, Missouri.

*Holotype*.—U.S.N.M. No. 108794a; paratypes, Nos. 108794b, c.

**BERKEIA MISSOURIENSIS, new species**

PLATE 16, FIGURES 11-14

This abundant species associated with *Pterocephalia* and *Burnetia* is one of the largest found. The slightly truncate glabella has three pairs of furrows. The very narrow fixigenes at the anterior end of the eye are only about one-fourth as wide as the glabella. On the other hand the brim is wide, equaling more than a third the glabellar length. In this species the eye lobes are only slightly curved. A small node occurs on the neck ring.

Davis formation; (loc. 11k) Federal Lead Mine No. 4, Flat River, Missouri.

*Holotype*.—U.S.N.M. No. 108795a; paratypes, Nos. 108795b, c.

UNCLASSIFIED GENERA

**ELVINIA** Walcott, 1924

**ELVINIA MONTIS, new species**

PLATE 18, FIGURES 1-4

*E. montis* is characterized by a normally tapered, truncate glabella. Two pairs of furrows are present, the rear pair taking a straight course in the middle third. The brim width is about half the length of the glabella exclusive of the occipital ring. It has a narrow rim, which at its widest point equals about half the preglabellar area. At the front end of the eye the fixigenes are half the glabellar width. Back of the rather strongly bowed eyes, which slope outward at an angle somewhat greater than the course of the dorsal furrow, the fixigenes expand into wide posterolateral limbs. On the outer surface none of the furrows are deeply impressed, and the surface apparently is smooth.

It was hoped that this form would turn out to be *E. tetouensis*, the species previously known from western Wyoming. Unfortunately it proved impossible to place it in that species owing to the more truncate glabella, less evenly curved glabellar furrows, and more strongly bowed eyes.

Snowy Range formation; (loc. 37r) Warm Spring Creek, Wind River Range, Wyoming.

*Holotype*.—U.S.N.M. No. 108812a; paratype, No. 108812b.



**ELVINIA UTAHENSIS, new species**

PLATE 18, FIGURES 5, 6

Except for the fact that this is such an important element of the fauna, this peculiarly weathered cranidium would have awaited the finding of additional material before its description. Strangely enough, this is the only *Elvinia* specimen found in large collections from the locality. In spite of its poor preservation this cranidium allows the specific characteristics to be ascertained.

The glabella tapers forward at a normal rate to a truncate front. Only a very shallow rear pair of furrows is visible, and the wide occipital furrow is also shallow. The brim, occupying nearly a third of the cranidial length, is separated into a thickened rim and a slightly wider convex preglabellar area. Eyes normal in size and position, and are not strongly bowed. The posterolateral limbs are long.

St. Charles limestone; (loc. 54e) Blacksmith Fork, Bear River Range, Utah.

*Holotype*.—U.S.N.M. No. 108813.

**ELVINIA RUEDEMANNI, new species**

PLATE 18, FIGURES 7-10

Ruedemann identified this form as *E. matheri*. However, very considerable differences in brim structure and the granulated surface exist. It is not certain that the larger and smaller cranidia here illustrated belong to the same species, for none of the smaller heads is well preserved, although it is clear that they are granulated. *E. ruedemanni* belongs to a group which may eventually have to be separated from *Elvinia*, but at present the altered appearance resulting from depression of the preglabellar area does not seem to warrant such action.

*E. ruedemanni* is characterized by a rather rapidly tapering glabella. Two pairs of furrows are developed, the anterior pair being short and shallow while the deeper rear pair is connected as usual. The rather large eyes are so far forward that their anterior ends are on a line with the front margin of the glabella. At this point the fixigenes are more than half the glabellar width. Rearward the fixigenes expand less rapidly than the glabella, and extend into large posterolateral limbs. The brim occupies about one-fourth the cranidial length and consists of a thickened rim nearly circular in cross section. The rim is less than half the width of the depressed preglabellar area. The surface is covered with granules except on the preglabellar area where vertical anastomosing lines take their place.

Potsdam sandstone (Theresa member); Greenfield, west of Saratoga Springs, New York.

*Holotype and paratypes*.—New York S. M.; casts, U.S.N.M. Nos. 108814a-c.

**ELVINIA GRANULATA**, new species

PLATE 18, FIGURES 11, 12

This cranidium, lying next to a good example of *Berkeia affinis*, is the only one found.

The large glabella tapers slightly to a rounded front. Only the rear pair of furrows is developed. The eyes are situated well forward. At the anterior end of the eyes the fixigenes are about one-third the glabellar width. Posterolateral limbs large and long. The brim, divided about equally between the preglabellar area and the thickened, somewhat upturned rim, occupies about a fourth the cranial length. The surface is covered closely by evenly spaced and evenly sized granules which in the preglabellar area overlies a system of vertical anastomosing lines.

Secret Canyon shale; (loc. 63) northeast of Adams Hill, Eureka District, Nevada.

*Holotype*.—U.S.N.M. No. 108815.

**ELVINIA MISSOURIENSIS** Resser

PLATE 18, FIGURES 13-17

*Elvinia roemeri* BRIDGE (part), U. S. Geol. Surv. Prof. Pap. 186-M, p. 251, pl. 69, figs. 12, 13, 1937.

*Elvinia missouriensis* RESSER, Smithsonian Misc. Coll., vol. 97, No. 10, p. 31, 1938.

A well-preserved cranidium, the pygidium, and the librigenae are figured to illustrate specific characteristics not shown in the holotype. It will be observed that the doublure evidently extends completely across the head.

Davis formation; (loc. 11k) Federal Lead Mine No. 4, Flat River, Missouri.

*Holotype*.—U.S.N.M. No. 93011; plesiotypes, No. 108819.

**ELVINIA GREGALIS**, new species

PLATE 18, FIGURES 18-23

This is one of the smaller species of the genus but seems to be rather widespread in the Wichita Mountains.

The glabella tapers at a normal rate to a truncate front margin. A shallow rear glabellar furrow is developed. The fixigenes average

about half the glabellar width. In front of the eye the suture diverges little, but back of the eye it forms posterolateral limbs of normal shape.

The brim, almost exactly a third of the cranial length, has a somewhat thickened rim considerably narrower than the preglabellar area. Longitudinally the considerable convexity is attained by a sharp bend about the midpoint. In cross section the relief is not so great, as the nearly flat fixigenes slope less steeply, and the glabella is gently arched. The anterior angles are not greatly depressed. The associated pygidium is characterized by the usual large, stout axis standing well above the pleural platforms and terminating very abruptly in the rear. Deep pleural furrows rib the slightly convex pleural platforms. The border turns up sharply all around.

Honey Creek limestone; (loc. 9q) Blue Creek Canyon, and other localities in the Wichita Mountains, Oklahoma.

*Holotype*.—U.S.N.M. No. 108816a; paratypes, Nos. 108816b, c.

#### ELVINIA LONGA, new species

PLATE 18, FIGURES 24-27

This species resembles *E. gregalis* but must be regarded as distinct owing to greater relative and absolute relief and its longer glabella.

The long glabella appears to be slender. It tapers at a normal rate to a rounded front margin. In spite of considerable relative relief the glabellar furrows are very shallow. At the anterior end of the eye the fixigenes are considerably more than half the glabellar width. Their width is not greatly increased either forward or backward and the posterolateral limbs are not so long. The brim occupies about one-fourth the cranial length, which makes it relatively narrower than in *A. gregalis*. Both the rim and the preglabellar area are strongly convex, the rim occupying a little more than a third the brim width. Longitudinally the cranium is decidedly convex, being slightly curved in the rear half and sharply curved in the front portion. Since the glabella and fixigenes are both convex, and the anterior angles sharply depressed, the lateral convexity is great.

Honey Creek limestone; (loc. 9p) Blue Creek Canyon, Wichita Mountains, Oklahoma.

*Holotype*.—U.S.N.M. No. 108817a; paratype, No. 108817b.

#### ELVINIA BRIDGEI Resser

PLATE 18, FIGURES 28-31; PLATE 19, FIGURES 1-5

*Elvinia roemeri* BRIDGE (part), U. S. Geol. Surv. Prof. Pap. 186-M, p. 251, pl. 69, figs. 19-21, 1937.

*Elvinia bridgei* RESSER, Smithsonian Misc. Coll., vol. 97, No. 10, p. 31, 1938.

Additional specimens of this species are figured to illustrate characteristics of pygidium and the peculiar flatness of the head.

Honey Creek limestone; (loc. 12p) 4 miles southeast of Hennepin, and other localities in the Arbuckle Mountains, Oklahoma.

*Cotypes*.—U.S.N.M. Nos. 93025a, b; plesiotypes, Nos. 108818a, b, 108820a, b.

**ELVINIA VAGANS, new species**

PLATE 19, FIGURES 6-9

Cranidium, exclusive of posterolateral limbs, nearly quadrate. Glabella, tapered to a slightly rounded frontal outline, is a little more than two-thirds the glabellar length. Brim divided about equally between a well-defined, slightly upturned rim, and preglabellar area. At their narrowest point the fixigenes are about one-third the glabellar width. Anterior to the eyes the facial suture diverges moderately to form rather square anterior angles. Posterolateral limbs long and stout. The moderately bowed eyes are a little less than one-third the cranial length and are set nearly parallel to the lateral dorsal furrow. Occipital furrow deep both on glabella and posterolateral limbs. Rear glabellar furrow shallow, others not developed. Laterally the glabella stands above the fixigenes with gentle curvature. Fixigenes nearly flat. Longitudinally the head has considerable convexity attained by an angulation near the midpoint. Each half individually is nearly in a plane, except for the furrows and raised rim. Associate pygidium normal in all respects. The wide axis reaches nearly to the rim. Three axial furrows are well developed. The nearly flat pleural platforms have two wide shallow furrows and a thickened and raised border.

Honey Creek limestone; (loc. 9q) 15 miles northwest of Fort Sill, Wichita Mountains, Oklahoma.

*Holotype*.—U.S.N.M. No. 108821a; paratype, No. 108821b.

**ELVINIA BREVIFRONS, new species**

PLATE 19, FIGURES 10-14

This species is so constricted in brim width and length that it is no longer fully characteristic of *Elvinia*. Cranidium as a whole forms a truncated isosceles triangle. The long glabella which tapers to a truncated front, with slightly rounded anterior angles, is demarcated by a shallow dorsal furrow. Brim width equals about one-fourth the glabellar length and has a nearly straight front outline. The occipital and rear glabellar furrows are deep. Measured at the same point the fixigenes are about half the width of the glabella. In front of the

eyes the facial suture diverges slightly. Eyes of moderate size, situated rather far forward, so that their anterior ends are about opposite the front of the glabella. They are only slightly bowed, but the palpebral lobes lie entirely outside the margin of the fixigene and are set at an angle slightly greater than the course of lateral dorsal furrow. Heavy but low eye ridges are developed. Viewed from the front the cranidium is evenly convex, with glabella and fixigenes forming one curved slope. Longitudinally the convexity is greater but is also even, except for the slight flattening of the brim toward a horizontal position. The associated librigena has a large ocular platform, a raised thickened rim, and a slender genal spine.

Honey Creek limestone; (loc. 12p) 4 miles east of Alpers, Arbuckle Mountains, Oklahoma.

*Holotype*.—U.S.N.M. No. 108822a; paratypes, Nos. 108822b, c.

**TAENICEPHALUS** Ulrich and Resser, 1924

**TAENICEPHALUS** PEALEI, new species

PLATE 19, FIGURES 15-23

Limestone layers in the Dry Creek formation cropping out from Logan eastward to the Bridger Range, and thence southeastward beyond Livingston, contain a species of *Taenicephalus*, often occurring in abundance. Most of the rock is a chowder, but here and there cranidia and other parts escaped being broken before entombment.

This species is characterized by normal features throughout. The glabella tapers at a normal rate. On the outside two pairs of shallow furrows may be traced, but on exfoliated examples three pairs are clearly visible. Where the test remains, the dorsal furrow is rather deep but narrow, and the occipital furrow is prominent both across the glabella and on the large posterolateral limbs. The fixigenes are half the glabellar width at the anterior end of the eyes. Brim width equals half the glabellar length. Preglabellar area rather wide and strongly convex. Rim expanded forward in middle, giving the anterior outline an angulated appearance. Eyes of moderate size and in normal position.

The pygidium is of normal size and oval shape. The almost completely exfoliated example figured has deeper furrows and greater relief than the exterior would show. The wide axis extends nearly the full length of the tail.

Although the outside of test seems to be smooth, the preglabellar area and other elevated portions of exfoliated specimens exhibit



scattered granules. Beneath the anterior furrow a somewhat irregular row of granules is present.

Dry Creek shale; (loc. 153) north of Gallatin River, east of Logan, Horseshoe Hills; (locs. 147a, 151, 152) Churn and Cottonwood Canyons, Bridger Range; Davis Creek, south of Livingston, Snowy Range, Montana.

*Holotype*.—U.S.N.M. No. 108823a; paratypes, Nos. 108823b-g.

#### TAENICEPHALUS HOLMESI, new species

PLATE 19, FIGURES 24-27

The glabella which tapers to a rounded front, has three pairs of fairly deeply impressed furrows. The brim width exceeds more than half the glabellar length. At the center the brim is divided about equally between rim and preglabellar area, both of which have about the same convexity. At the eye the fixigenes are almost exactly equal to half the glabellar width. The small eyes are situated about the midpoint of the cranidium. They are very strongly bowed in a longitudinal direction, which, together with the distinctness of the palpebral lobe, projects the eyes considerably above the remainder of the cranidium. In cross section the glabella is moderately, and the fixigenes greatly, curved. Although individual parts have high relief the longitudinal curvature is not great and is rather evenly distributed. The pygidium, typical in size and shape, has considerable convexity.

The specific name is given in recognition of the geologic work done by the collector, Dr. W. H. Holmes.

Dry Creek shale; (loc. 66x) Gallatin Valley, northwestern Yellowstone National Park, Wyoming.

*Holotype and paratypes*.—U.S.N.M. No. 9595.

#### TAENICEPHALUS SPECIOSUS, new species

PLATE 20, FIGURE 19

This rather large species found in the northeastern part of the Yellowstone National Park differs from *T. holmesi* in that all furrows are shallower, and the brim is wider. Also, the glabella and fixigenes are less highly arched in both directions. The surface is smooth.

Dry Creek shale; (loc. 62r) Abiathar Mountain, northeastern Yellowstone National Park, Wyoming.

*Holotype*.—U.S.N.M. No. 108831a; paratype, No. 108831b.

**TAENICEPHALUS LIBERTYENSIS**, new species

PLATE 19, FIGURES 28-32

Several cranidia, a librigena, and several small pygidia are contained in the collection from this locality. Only the larger of the specimens have been figured. The species is characterized by normal shape and development of the several parts, with the possible exception of a flattening in the preglabellar area. The glabella tapers at a normal rate. On the outer surface its anterior outline is straighter than on exfoliated specimens, a condition due to widening of the dorsal furrow in the latter instance. Two pairs of furrows show on the outside and three on the inside of the test. The deep occipital furrow is irregular. The neck ring has a small spine. Fixigenae are about half the glabellar length exclusive of the occipital ring. Rim slightly elevated and thickened, expanding forward somewhat in the middle where it is only slightly less wide than the preglabellar area. Eyes are normal size and moderately bowed. In cross section the curvature is not great in the central portion of the cranidium. In spite of the depressed anterior angles the front margin is nearly straight but has considerable relief because of the greatly depressed posterolateral limbs. Librigena normal in size and shape, with a rather wide and possibly short genal spine. The associated pygidium is normal in all respects.

St. Charles limestone; (loc. 56g) 6 miles west of Liberty, Bear River Range, Idaho.

*Holotype*.—U.S.N.M. No. 108824a; paratype, No. 108824b.

**TAENICEPHALUS CORDILLERENSIS** Miller

PLATE 19, FIGURE 33

*Taenicephalus cordillerensis* MILLER, Journ. Pal., vol. 10, No. 1, p. 33, pl. 8, figs. 40, 41, 1936.

Many of the fossils of this zone are found on weathered surfaces. The illustrated example shows several cranidia in various states of preservation and part of a librigena.

Snowy Range formation; (loc. 37r) Warm Springs Creek, Wind River Range, Wyoming.

*Holotype*.—Columbia Univ. No. 12622; plesiotype, U.S.N.M. No. 108825.

**TAENICEPHALUS GRANULOSUS**, new species

PLATE 20, FIGURES 4-7

This moderately large species is covered with rather large, evenly distributed granules.

The glabella tapers considerably to a narrow truncate front. Three pairs of glabellar furrows are deeply impressed, and the occipital furrow and ring are strongly developed. The brim width exceeds a third of the cranial length, and the preglabellar area is somewhat wider than the rim at the center. At the eye the fixigene is about one-third the glabellar width. Longitudinally the head is only slightly convex, except that the fixigenes are flexed at the palpebral lobe. In cross section the glabella is moderately convex, with a slight indication of a keel, while the fixigenes are very convex. Both the rim and preglabellar area are highly convex owing to the depth of both dorsal and anterior furrows. Posterolateral limbs bent down rather sharply.

St. Charles limestone; (loc. 4y) Two Mile Canyon, south of Malad, Wasatch Mountains, Idaho.

*Holotype*.—U.S.N.M. No. 108828a; paratypes, No. 108828b.

#### TAENICEPHALUS MALADENSIS, new species

PLATE 20, FIGURES 8-10

Associated with *T. granulosus* is a smaller form with shallower furrows. Its surface is not granulose but ornamented by raised anastomosing lines, which form a more or less reticulate network. Neither the fixigenes nor the preglabellar area is as convex, which gives *T. maladensis* a smoother appearance than *T. granulosus*.

St. Charles limestone; (locs. 54x, 4y) Two Mile Canyon, south of Malad, Wasatch Mountains, Idaho.

*Holotype*.—U.S.N.M. No. 108826a; paratype, No. 108826b.

#### TAENICEPHALUS ORNATUS, new species

PLATE 20, FIGURES 11, 12

Several species of *Taenicephalus* have been collected in Blacksmith Fork canyon. They were not found at the same spot and therefore may occur at somewhat different levels. Several cranidia, characterized by an ornate appearance due to the conspicuous granulation and deep furrows as well as to the relatively high relief, may appropriately be named *T. ornatus*. The rather wide glabella tapers at the average rate of a rounded front and has three pairs of furrows rather deeply impressed on the outside of the test. The slightly convex fixigenes average nearly half the glabellar width. The brim is about one-third the cranial length. A deep anterior furrow separates the somewhat thickened and considerably elevated rim which expands forward in the center from a preglabellar area of nearly equal width. The rather small and very sharply bowed eyes are prominent because the palpebral lobe projects outward and the fixigenes are arched at the eyes.

Longitudinally the relief of the cranidium is not great but because both the dorsal and anterior furrows are deep the relative relief between the several parts is accentuated. In cross section the convexity of the glabella and sharp rise of the fixigenes to the eyes as well as sharp depression of anterior angles and posterolateral limbs, give both the front and rear margins of the head considerable curvature. The surface is covered by evenly spaced granules.

St. Charles limestone; (loc. 54e) Blacksmith Fork, Bear River Range, Utah.

*Holotype*.—U.S.N.M. No. 108829.

#### TAENICEPHALUS STRIATIFRONS, new species

PLATE 21, FIGURES 1-3

The second species from the locality is characterized by a rather strongly tapering glabella and a vertically striated brim. The fixigenes are rather evenly covered by granules but only a few are found on the more elevated parts of the glabella. Brim width is considerably less than one-third the cranidial length. The longitudinal convexity is not great nor does the cross section attain high relief, even though the glabella and the fixigenes are convex.

St. Charles limestone; (loc. 54e) Blacksmith Fork, Bear River Range, Utah.

*Holotype*.—U.S.N.M. No. 108833a; paratype, No. 108833b.

#### TAENICEPHALUS UTAHENSIS, new species

PLATE 21, FIGURES 4-6

This third species from the locality is represented by several cranidia. It is most like *T. striatifrons* in shape and general appearance but differs in having considerably less surface ornamentation. The average size glabella tapers at a normal rate and has the usual sets of furrows faintly outlined. The brim width is just about one-third the cranidial length. The rim is about two-thirds the width of the preglabellar area in the center. Both are convex. The fixigenes are narrow and the eyes of normal size and shape. Longitudinally the head is not very convex, most of it being attained in the anterior portion. In cross section the fixigenes rise rather abruptly from the dorsal furrow. The anterior angles are considerably depressed but the posterolateral limbs are not.

St. Charles limestone; (loc. 54e) Blacksmith Fork, Bear River Range, Utah.

*Holotype*.—U.S.N.M. No. 108834a; paratype, No. 108834b.

**TAENICEPHALUS HYRUMENSIS**, new species

PLATE 20, FIGURES 13-18

This species is represented by a number of cranidia, a hypostoma, and several pygidia. It is characterized by the smoothness of the test. Slight indications of granulation are found on parts of the glabella and rim. They are more clearly developed on the preglabellar area. The rather long, fairly slender glabella tapers to a rounded front. Faint furrows are present on the test, but in exfoliated specimens three well-developed sets can be seen. Brim width less than half the glabellar length, divided by the anterior furrow into about equal parts. The fixigenes average less than half the glabellar width. Posterolateral limbs fairly large. Eyes of moderate size, moderately bowed. The associated pygidium is rather large and flat, approaching that of *Wilbernia* in several respects, but it lacks the pronounced doubleure of that genus. It is possible that this pygidium should be referred to *T. modestus* from the same locality.

St. Charles limestone; (loc. 55h) Blacksmith Fork, Bear River Range, Utah.

*Holotype*.—U.S.N.M. No. 108830a; paratypes, Nos. 108830b-c.

**TAENICEPHALUS MODESTUS**, new species

PLATE 21, FIGURE 7

A single cranidium is sharply demarcated from the other species at the locality. Its reference to *Taenicephalus* may be questioned because of the width of the cranidium across the brim and the flatness of the whole. However, it is closer to this genus than to *Elvinia*, which it most resembles. The glabella tapers at the normal rate and has average proportions. Several sets of furrows are faintly indicated, while the occipital furrow is rather deep. The brim width is half the glabellar length exclusive of the occipital ring. Both the preglabellar area and rim are convex and of about equal width. Fixigenes, eyes, and course of the suture are approximately normal, except that the anterior branch of the suture diverges slightly more than average.

St. Charles limestone; (loc. 55h) Blacksmith Fork, Bear River Range, Utah.

*Holotype*.—U.S.N.M. No. 108835.

**TAENICEPHALUS TEXANUS**, new species

PLATE 21, FIGURES 8-12

All of the 10 or more cranidia are normal in size and shape with a projecting front due to the forwardly expanded rim. The glabella



is about average in size and shape and has the usual three sets of furrows. The brim width is half of the glabellar length exclusive of the neck ring. Fixigenes are rather narrow, averaging a little more than a third of the glabellar width. Surface finely granulose.

Wilberns formation; (loc. 68) Packsaddle Mountain, 11 miles southeast of Llano; and (loc. 70) Baldy Mountain, 8 miles northwest of Burnet, Texas.

*Holotype*.—U.S.N.M. No. 108836a; paratypes, Nos. 108836b-d.

**TAENICEPHALUS WICHITAENSIS, new species**

PLATE 21, FIGURES 13-17

A number of cranidia occur in a coarsely granular limestone full of trilobite fragments. Much of the rock is nearly white, but it contains many particles of glauconite and most of the trilobites are stained red, which gives the rock a peculiar appearance. This species is normal in all respects. The fairly wide glabella is truncated in the front. All specimens are exfoliated, and on them three sets of furrows are visible. The neck ring expands, possibly bearing a short spine. The brim width exceeds the length of the glabella including the neck ring. It consists of a rim that expands rapidly forward in the middle from a nearly straight anterior furrow to give the front of the head a considerable projection. The rim shrinks to extinction at the anterior angles from the same width as the preglabellar area at the center while the latter maintains its width into the anterior angles. At the front end of the eye the fixigenes are less than half the glabellar width, an average which they maintain throughout. The fairly large eyes are in normal position for the genus. Triangular posterolateral limbs are of considerable size. Surface of available exfoliated specimens smooth, as are the small fragments of test remaining.

Honey Creek limestone; (loc. 9q) Blue Creek Canyon, 15 miles northwest of Fort Sill, Wichita Mountains, Oklahoma.

*Holotype*.—U.S.N.M. No. 108837a; paratypes, Nos. 108837b-d.

**TAENICEPHALUS QUINNENSIS, new species**

PLATE 21, FIGURES 18-23

This species is represented by cranidia, librigenes, and a pygidium. Owing to greater width across the anterior part of the cranidium and the flatter relief in the brim, the species approaches *Elvinia* in appearance.

The fairly wide glabella, well rounded in front, has the usual sets of well-defined furrows, the rear pair being connected across the

middle by a wide bar. The brim width is just about half the glabellar length including the neck ring. The rim, not greatly expanded beyond the anterior angles, is much narrower than the preglabellar area. Fixigenes rather wide, averaging over three-fourths the glabellar width. Behind the eyes the sutures do not diverge rapidly, thus forming wide and rather short posterolateral limbs. Anterior to the eyes the divergence of the suture is not great, which leaves only moderate anterior angles. The eyes are fairly sharply bowed. The palpebral furrow in line with the facial suture has little curvature and a wide eye band; hence the eyes are prominent. Longitudinally the head does not have great convexity. Laterally, although both the glabella and fixigenes are convex, the total relief is not great. Anterior angles only moderately depressed and the posterolateral limbs even less.

Mendha limestone; (loc. 7j) 1 mile north of Italian Ranch foothills, Quinn Canyon Range, Nevada.

*Holotype*.—U.S.N.M. No. 108838a; paratypes, Nos. 108838b-d.

#### TAENICEPHALUS CASTLENSIS, new species

PLATE 21, FIGURES 24, 25

Several cranidia are in the small collection from this locality, which is situated between the Yellowstone Park and the occurrences of *Taenicephalus* species north of the Gallatin River. It is typical in most respects. The moderately long glabella tapers to a truncated front. Three pairs of furrows are sharply impressed on the exfoliated holotype, and the occipital furrow is wide. In the center the brim width is a little less than half of the glabellar length including the occipital ring. It consists of approximately equal subdivisions. The rim tapers rapidly to extinction at the anterior angles which are somewhat rounded. Both rim and preglabellar area have about the same degree of convexity. Anastomosing lines cover the preglabellar area, and a few scattered granules appear on the rim. Eyes, fixigenes, and posterolateral limbs are of normal size and proportions.

Dry Creek formation; (loc. 62s) Castle Peak, north of Squaw Creek, Gallatin Range, Montana.

*Holotype*.—U.S.N.M. No. 108839.

#### TAENICEPHALUS WYOMINGENSIS, new species

PLATE 21, FIGURE 32

A small collection from the Big Horn Mountains contains a good species of *Taenicephalus*. It is close to *T. cordillerensis* Miller from the Wind River Range but has a wider preglabellar area. Compared

with *T. holmesi*, the palpebral lobes are less prominent because the fixigenes are less sharply bowed at that point.

Snowy Range formation; head of Buffalo Fork, west side of Big Horn Mountains, Wyoming.

*Holotype and paratypes*.—U.S.N.M. No. 11593.

**TALBOTINA** Lochman, 1938

**TALBOTINA CANDIDA**, new species

PLATE 21, FIGURES 27, 28

The glabella covers somewhat less than half the cranidial area and is sculptured by three sets of recurved furrows and a deep, wide occipital furrow. The fixigenes average about half the glabellar width. Posterolateral limbs are fairly long and of normal width. The brim, about equal in width to the fixigenes, is separated into rim and preglabellar area. The somewhat swollen rim widens to the center, chiefly by rather sudden expansion rearward. The eyes, of average size, are situated behind the midpoint of the glabella. Eye lines present. Convexity is about average in amount, while the relief is pronounced. The surface is abundantly granulose. Libragene, thorax, and pygidium unknown.

Wilberns formation; (loc. 14b) Cold Creek, opposite north end of Sponge Mountain, Texas.

*Holotype*.—U.S.N.M. No. 108841.

**TALBOTINA ULRICHI**, new species

PLATE 21, FIGURE 26

A second species from Texas is characterized by being shorter and by the glabella in consequence occupying a relatively greater proportion of the cranidium. The anterior furrow also has a more even course near the center, although the rim remains proportionally about the same as in *T. candida*. The surface is nearly smooth.

Wilberns formation; (loc. 14b) Cold Creek, opposite north end of Sponge Mountain, Texas.

*Holotype*.—U.S.N.M. No. 108840.

**TALBOTINA CAELATA**, new species

PLATE 10, FIGURE 4

When the fauna from the locality was described, this cranidium was overlooked. *T. caelata* is a beautifully sculptured trilobite of medium size. It differs essentially from the genotype in its narrowness.

The large, well-demarcated glabella tapers at a normal rate to a rounded front. Two pairs of shallow recurved furrows are visible. The fixigenes at the anterior end of the eye are about half the glabellar width. The eye lines are made conspicuous by a furrow which parallels them on their front side. Brim about half the glabellar length exclusive of the occipital ring. A conspicuous, somewhat thickened rim widens backward in the center, greatly reducing the width of the preglabellar area. The moderate-sized eyes are not strongly bowed and are situated posterior to the middle of the cranidium. The cranidium has considerable relief in each separate part, as well as in its entirety. Longitudinally the cranidium stands high, with a fairly even curvature, slightly accentuated in the glabella. In cross section the glabella stands completely above the fixigenes. The fixigenes are rather strongly convex in lateral direction, having greatly depressed posterolateral limbs, with convexity increasing anterior to the eye lines.

Nolichucky shale; (loc. 27d) U. S. 11, 7 miles northeast of Rogersville, Tennessee.

*Holotype*.—U.S.N.M. No. 108734.

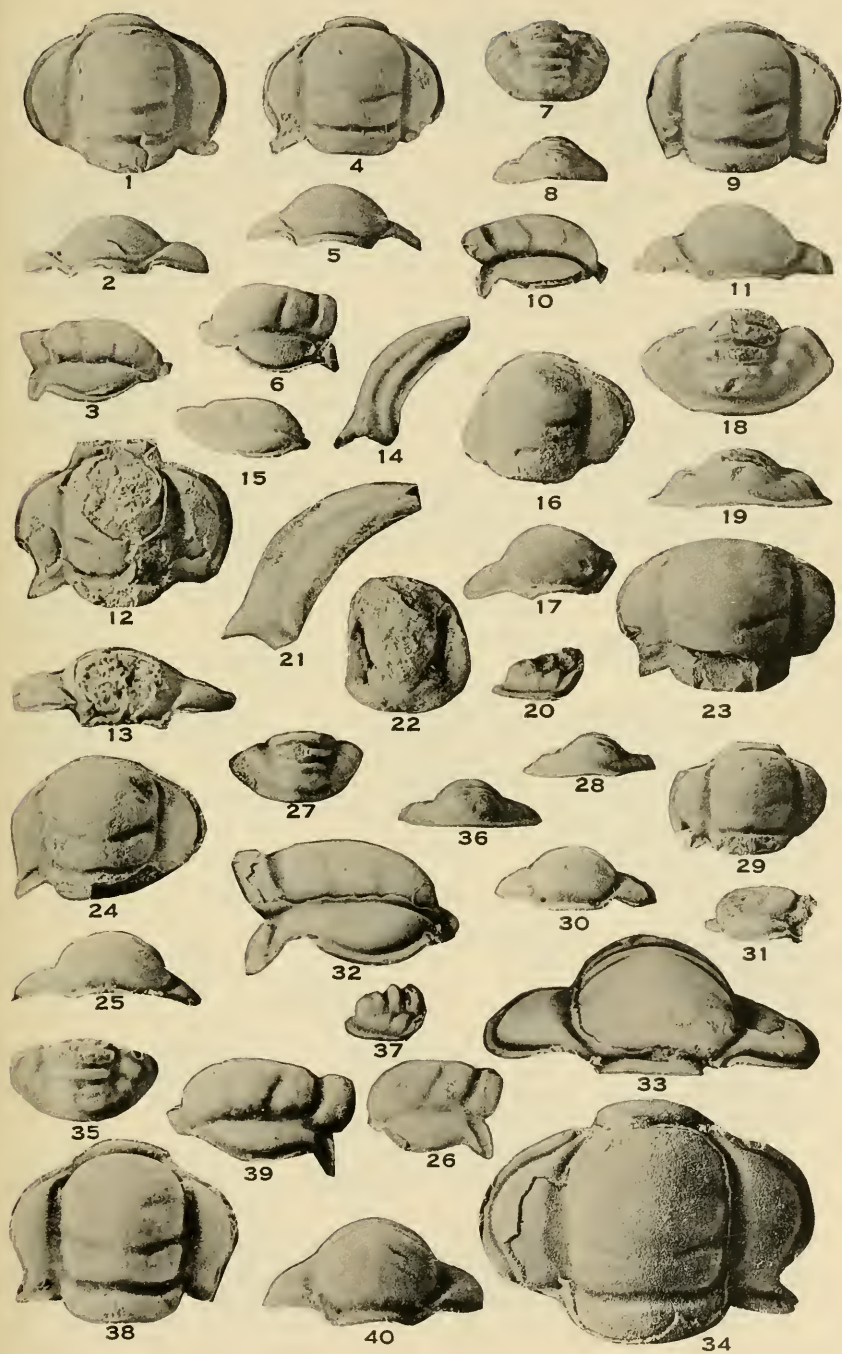
## EXPLANATION OF PLATES

Figures are natural size unless otherwise indicated. Since all the species described belong to the Upper Cambrian, only the formational names are given with the locality descriptions.

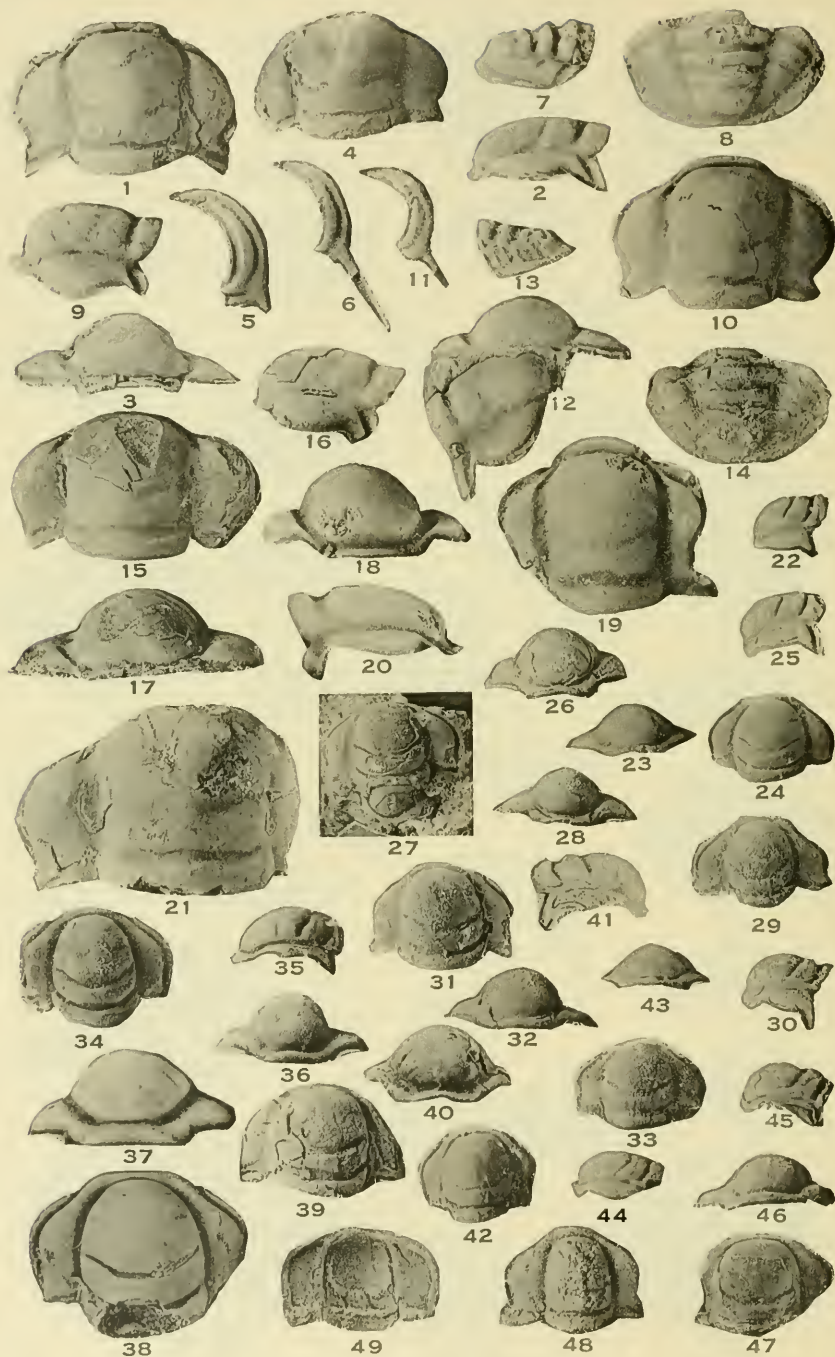


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UPPER CAMBRIAN TRILOBITES



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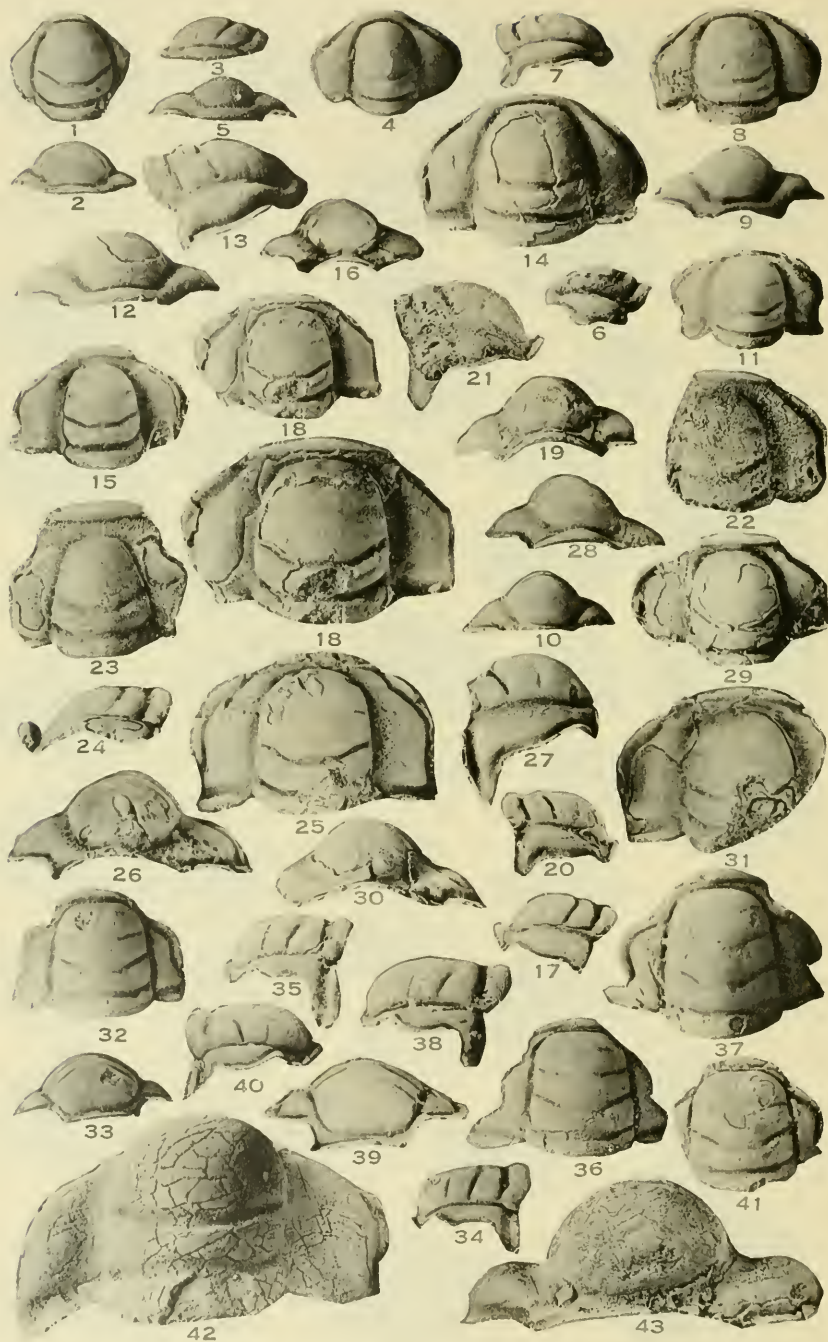
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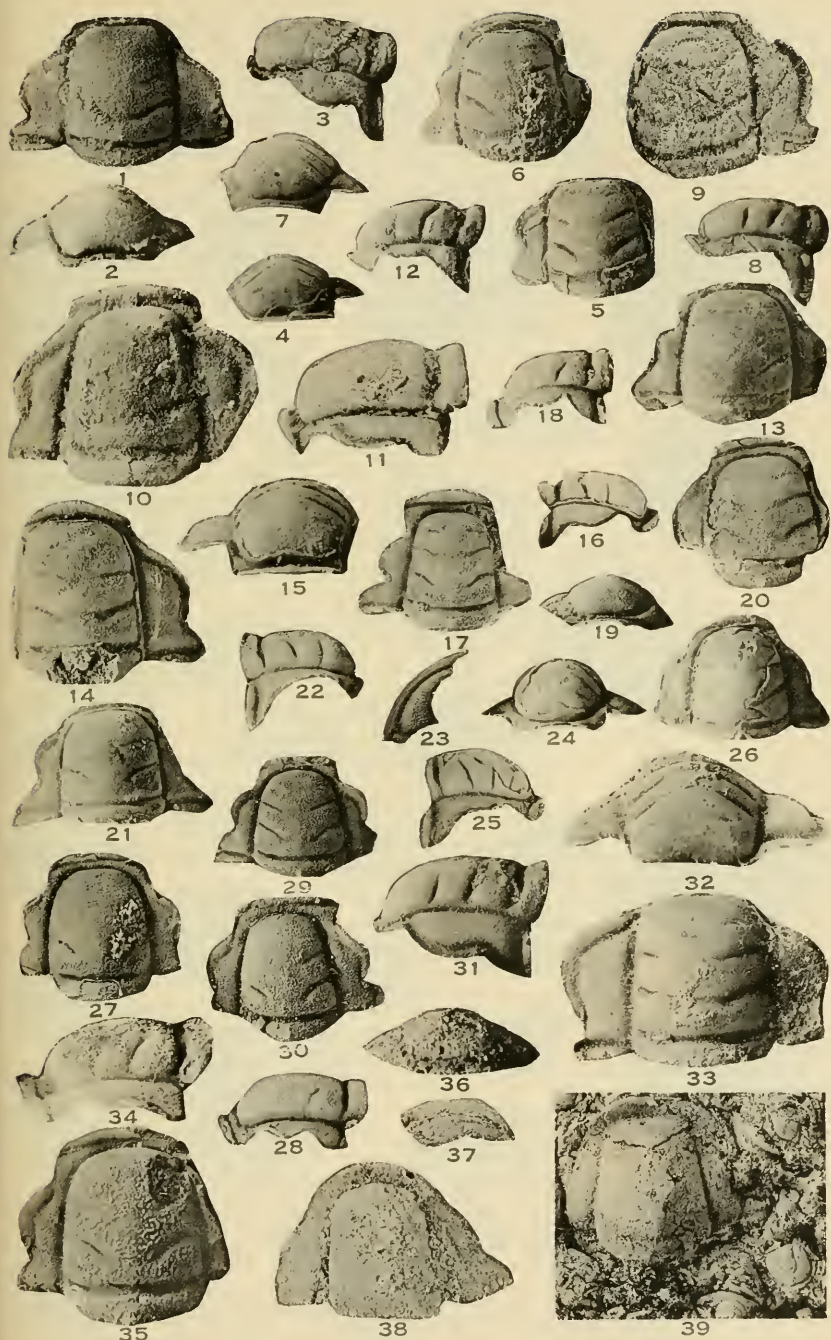
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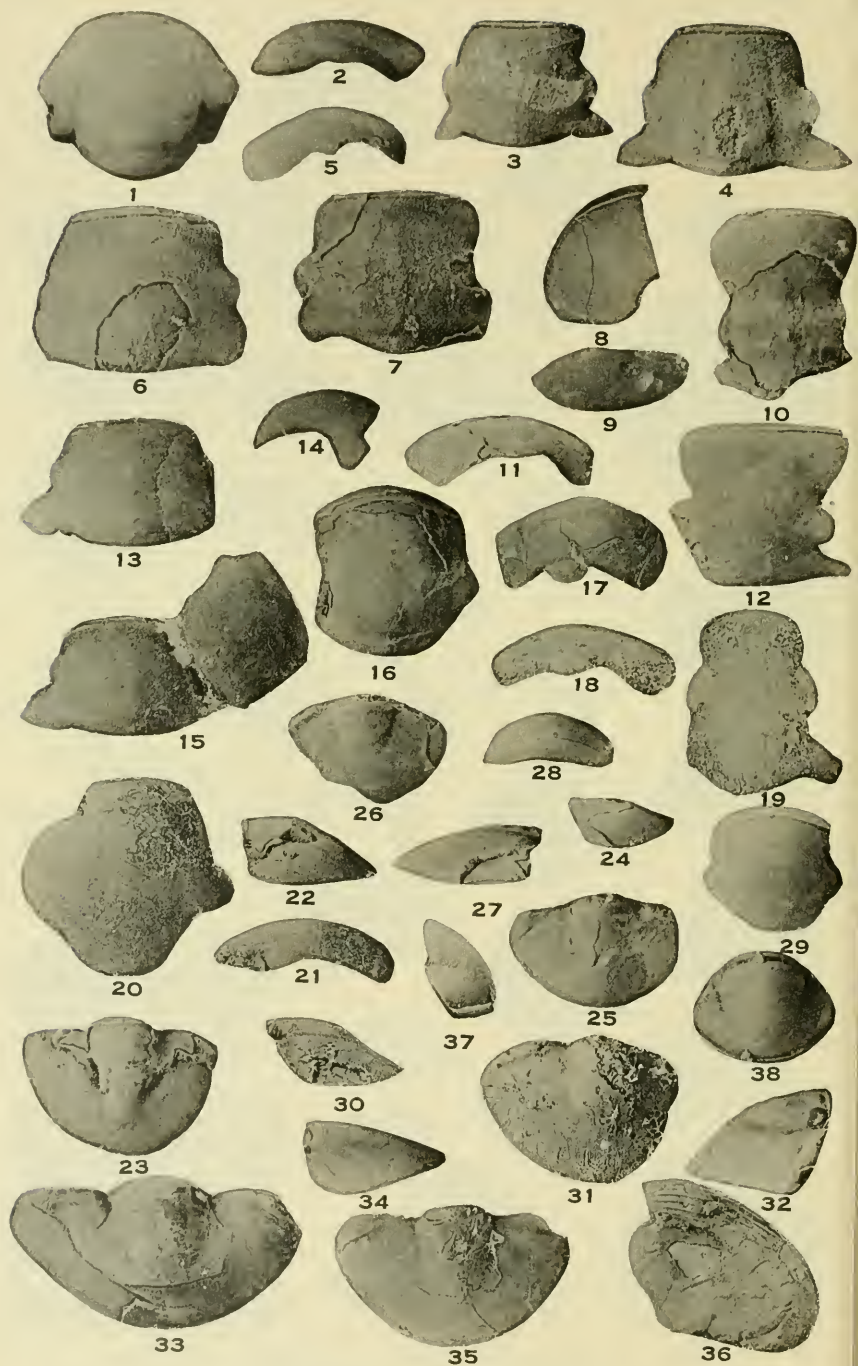
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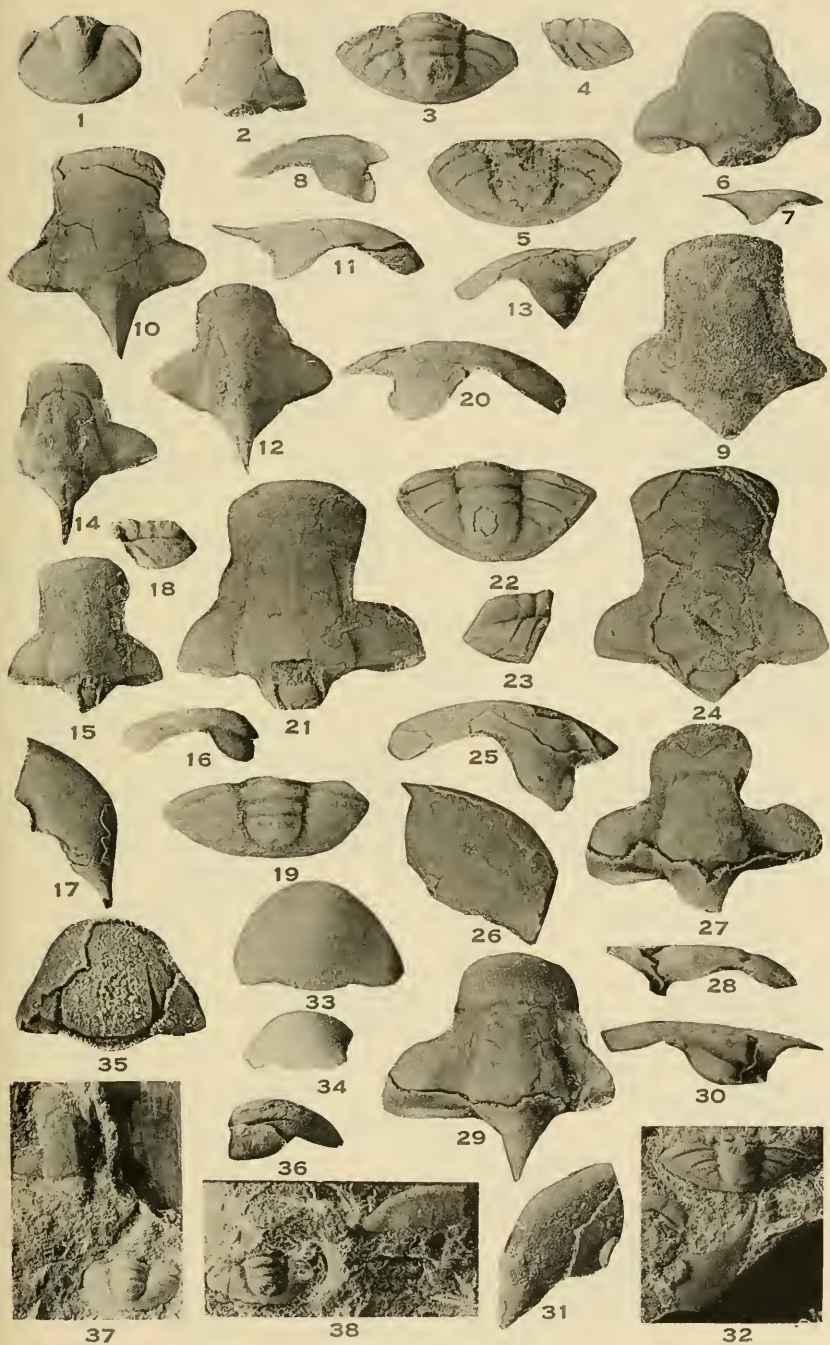
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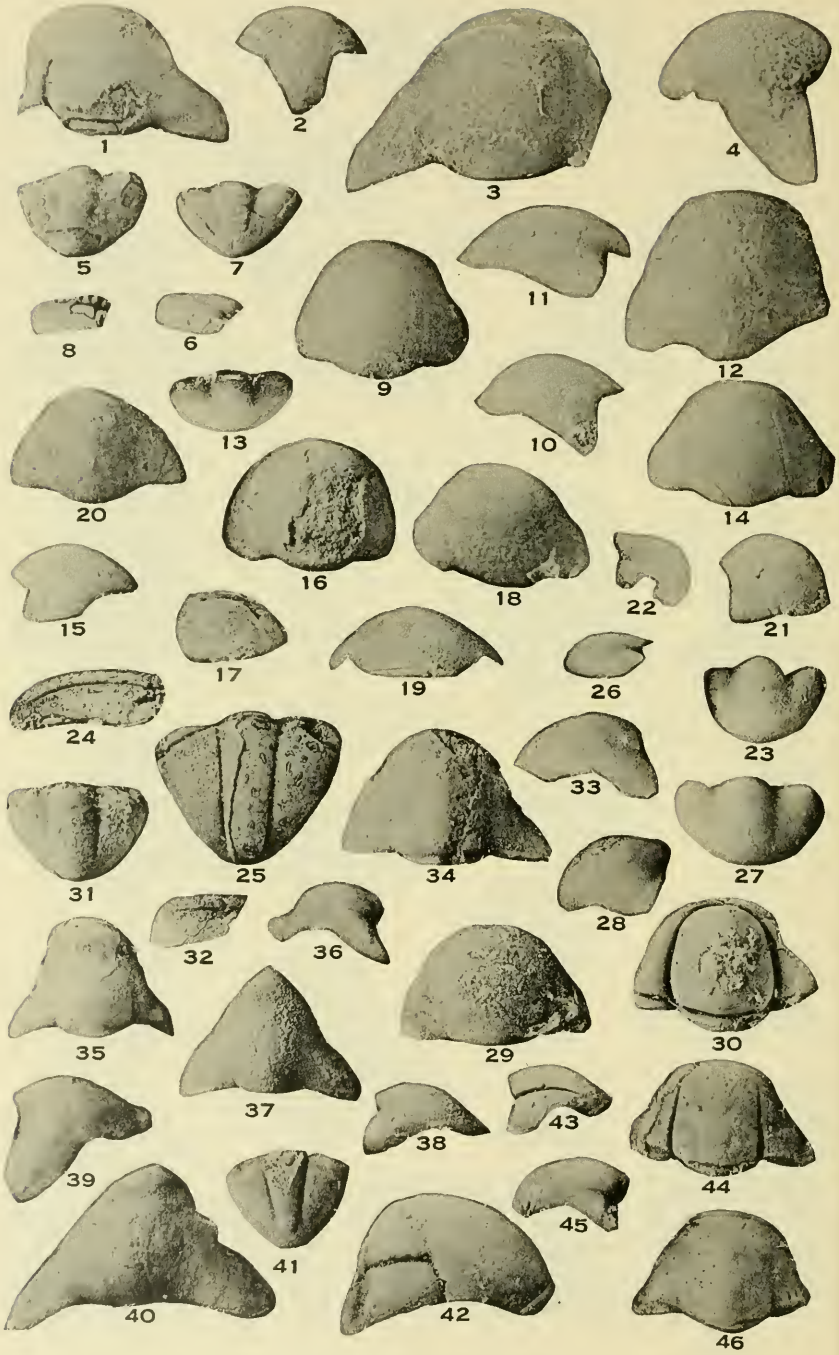
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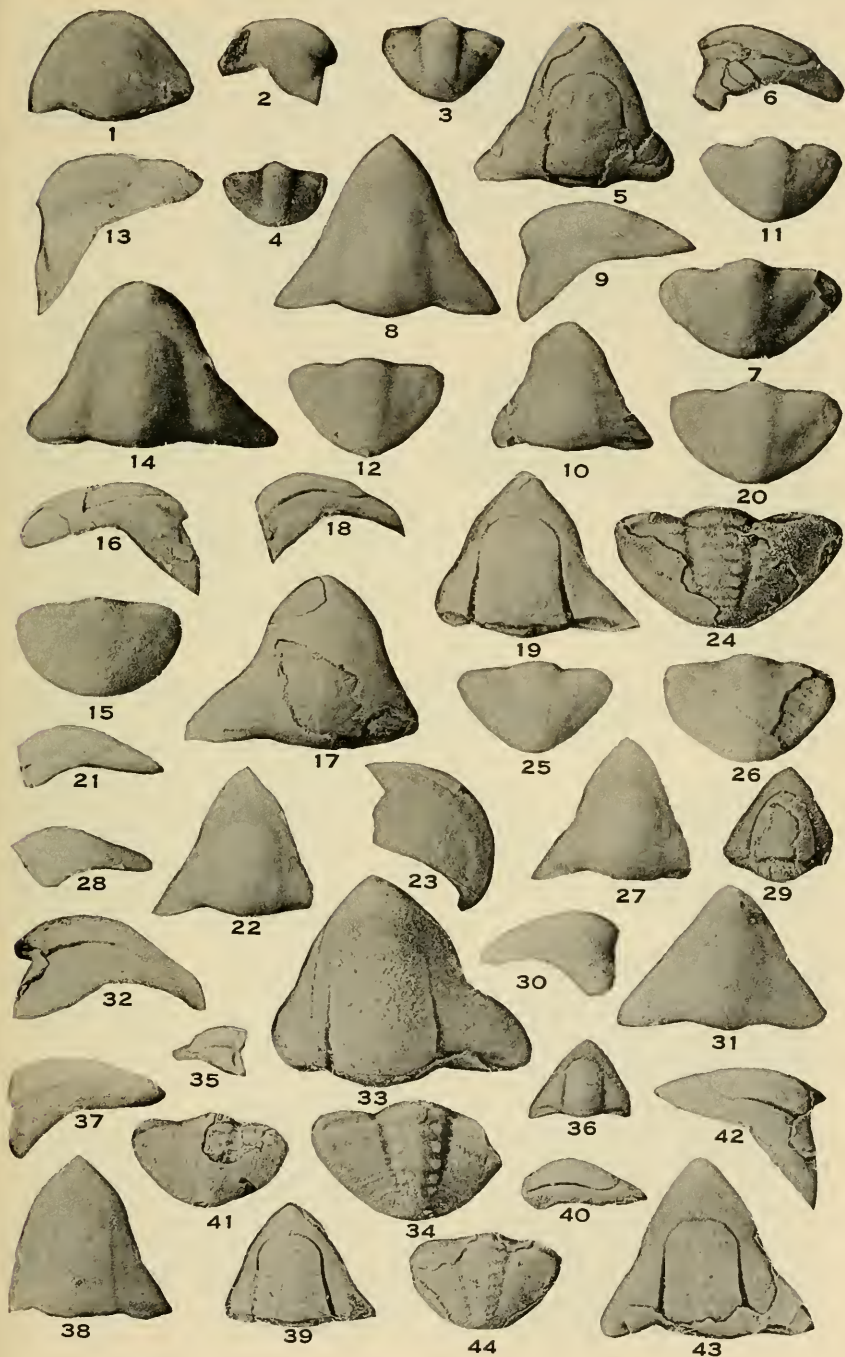


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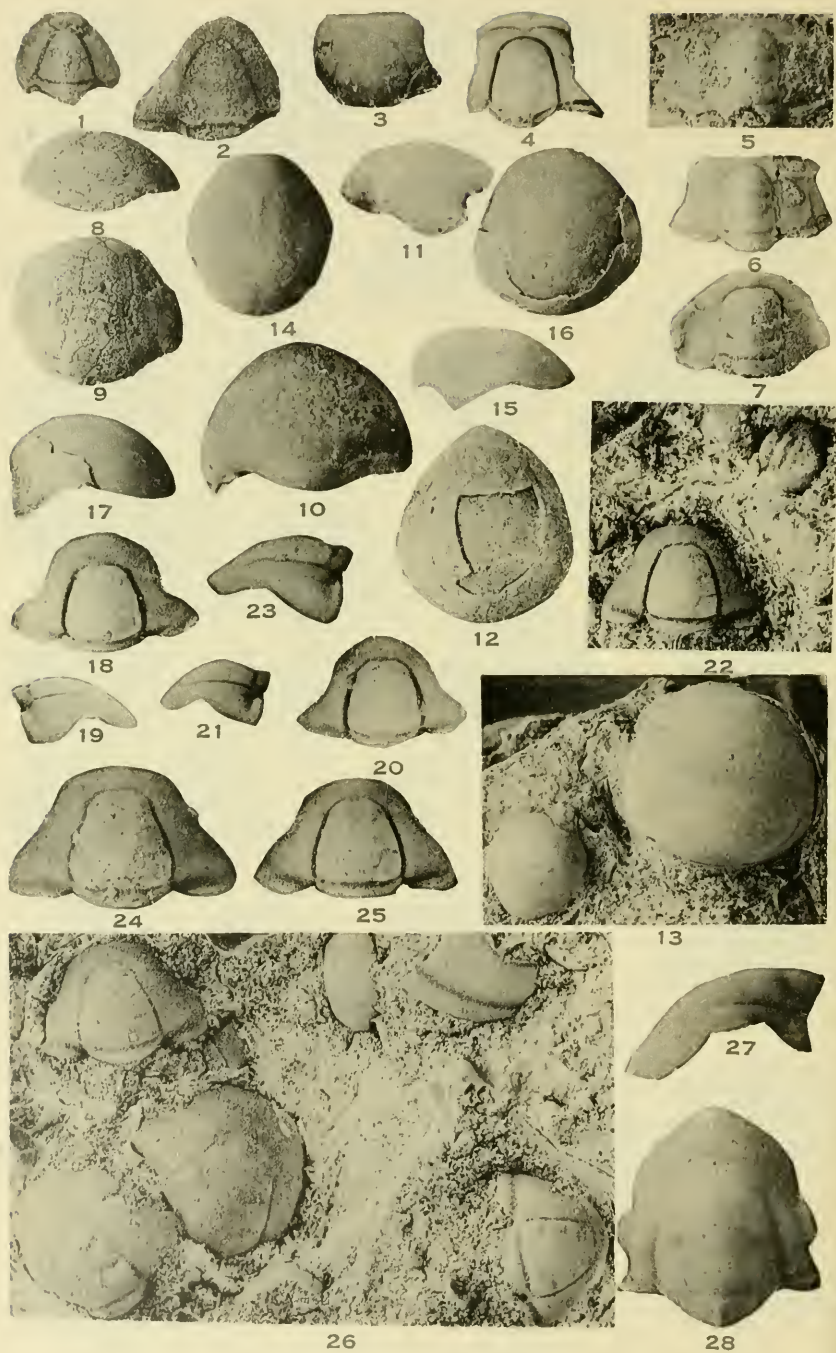
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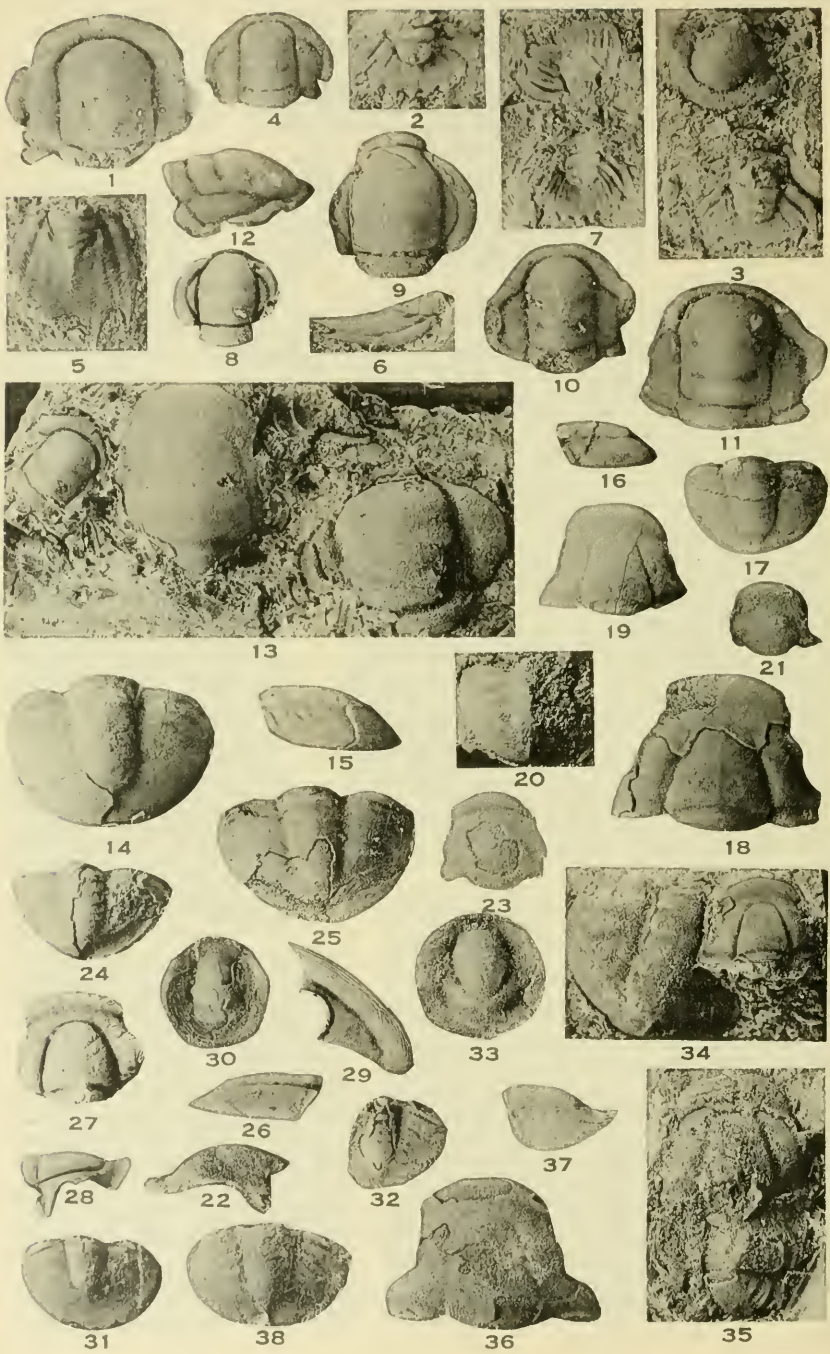


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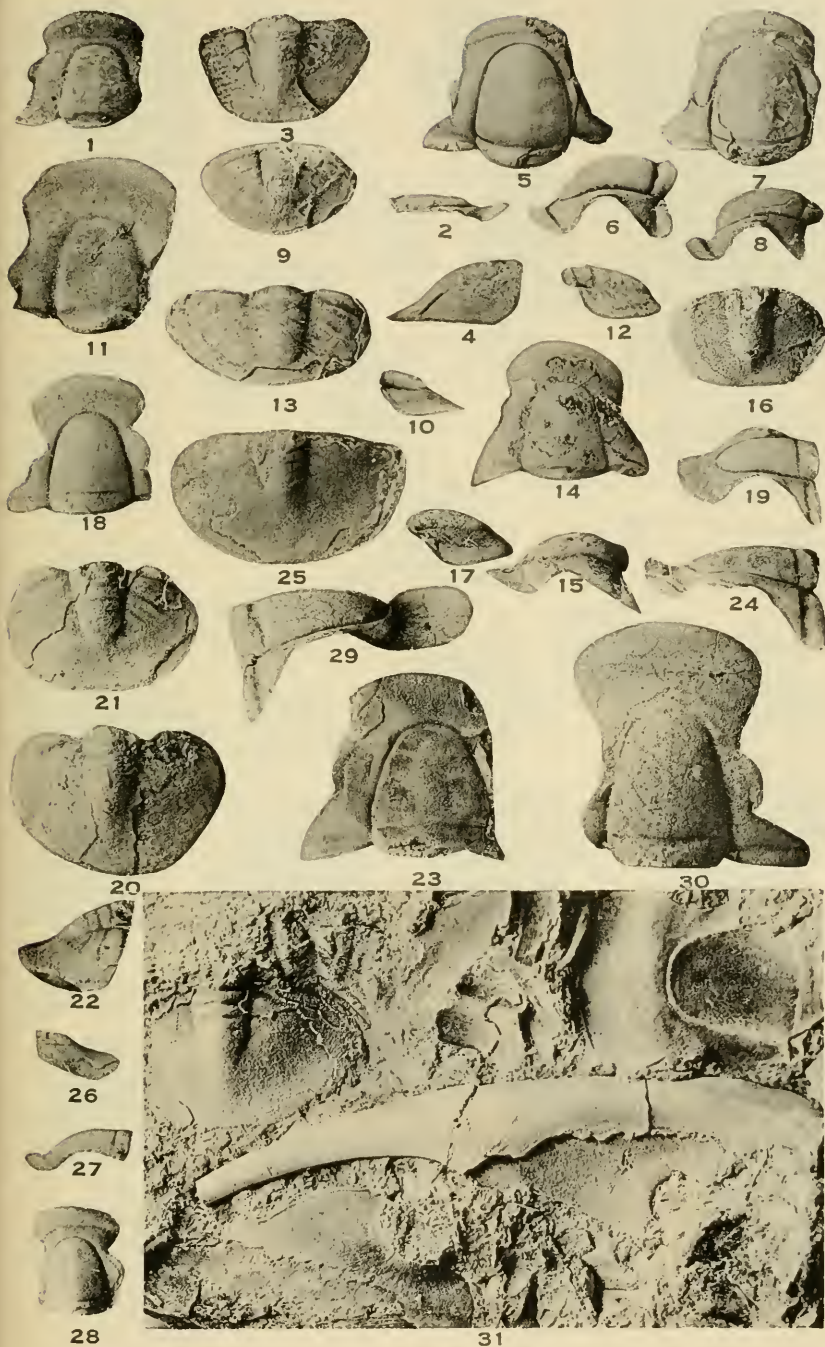
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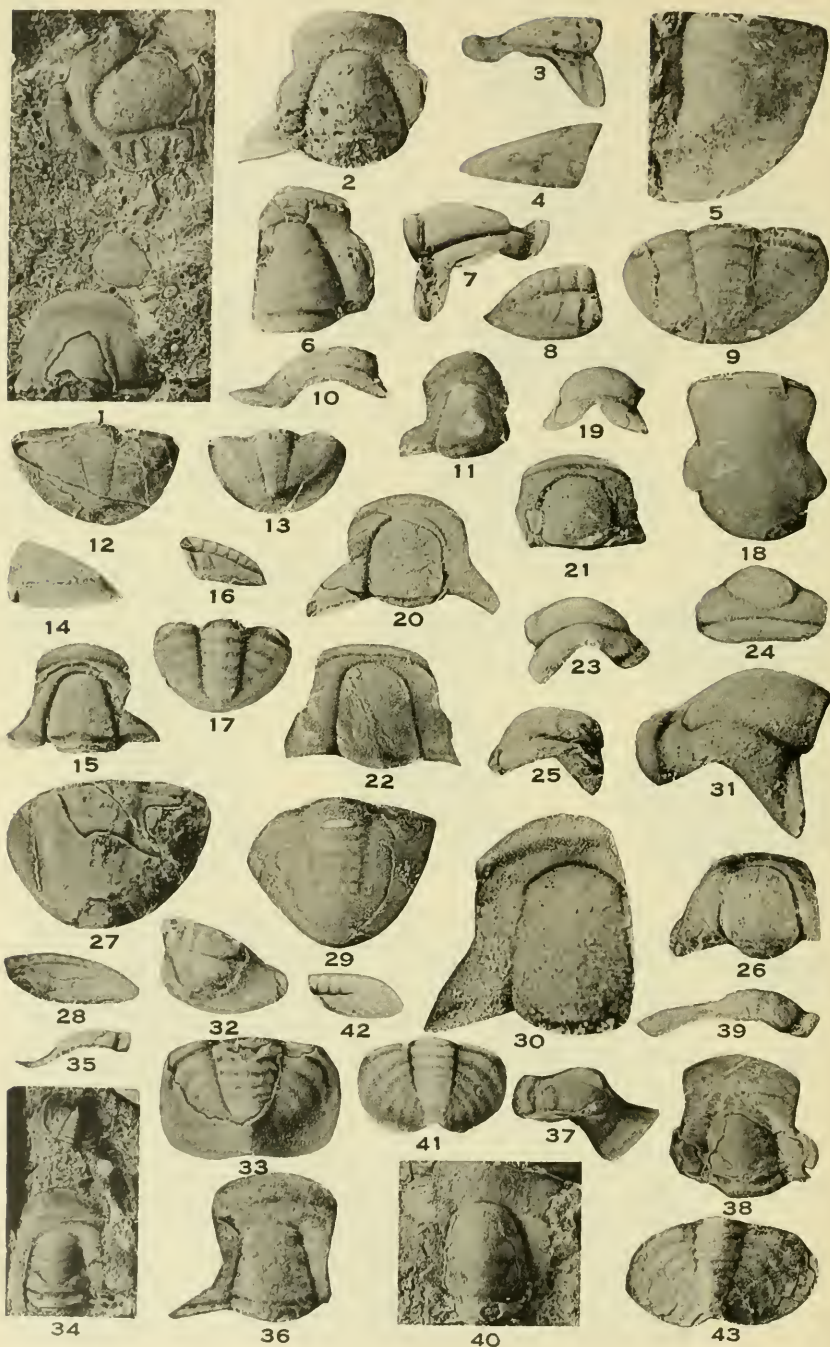
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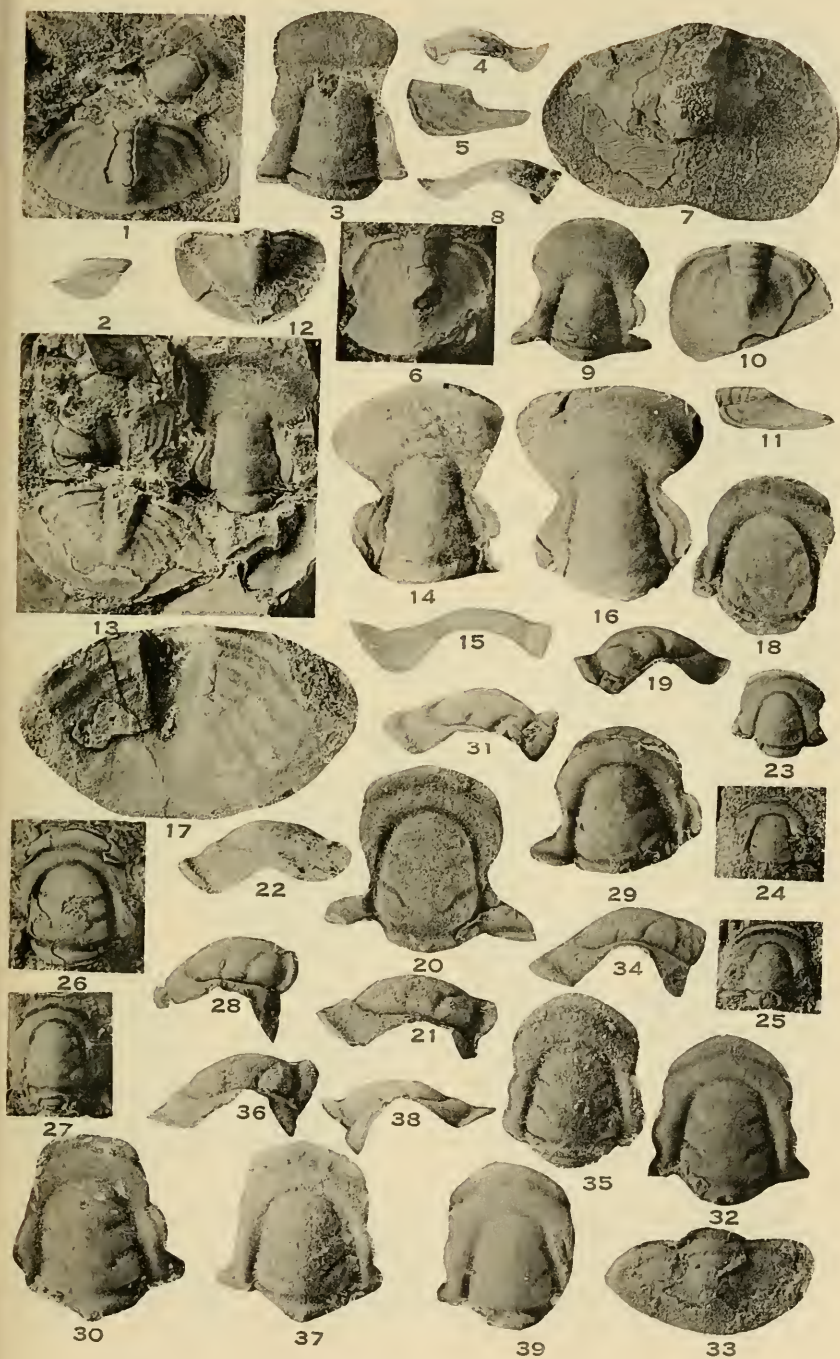


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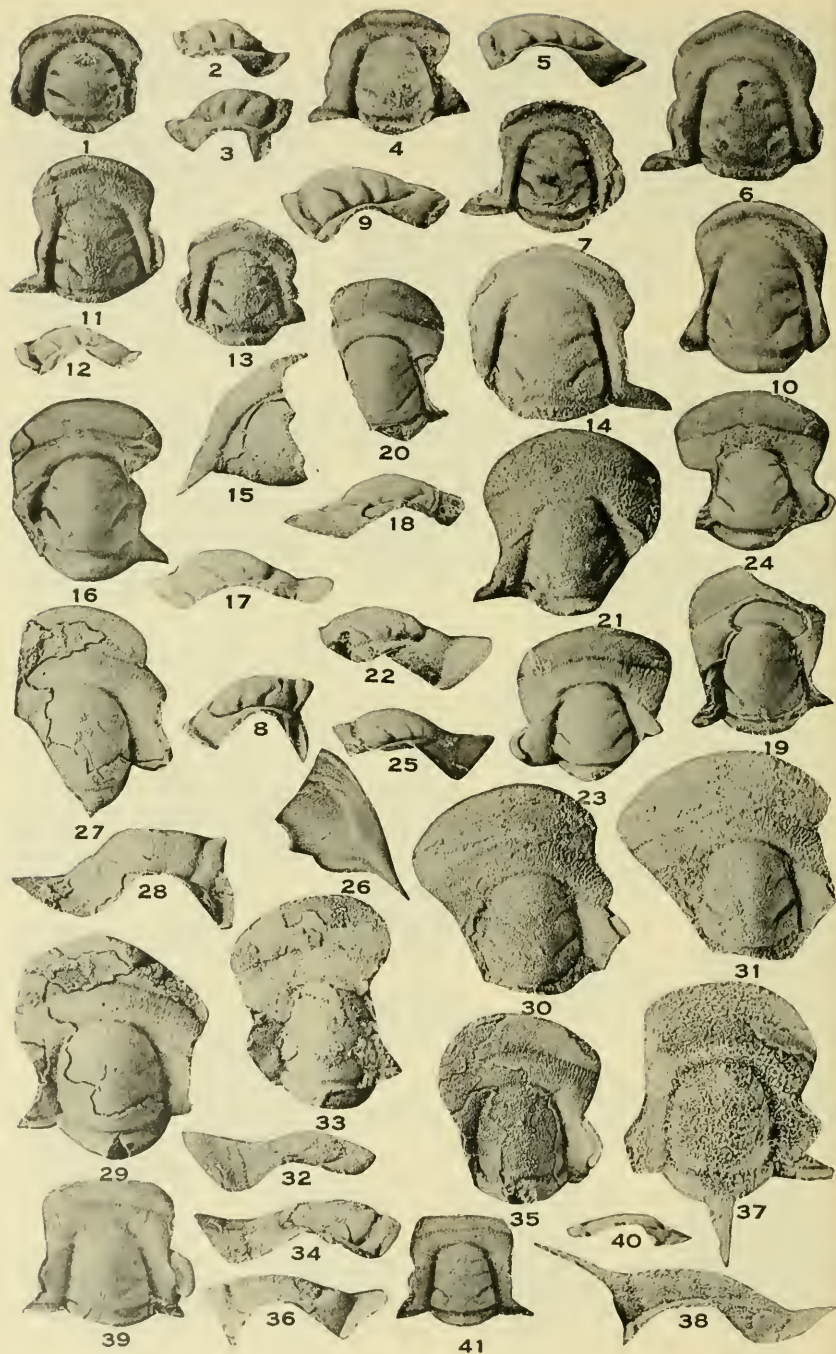
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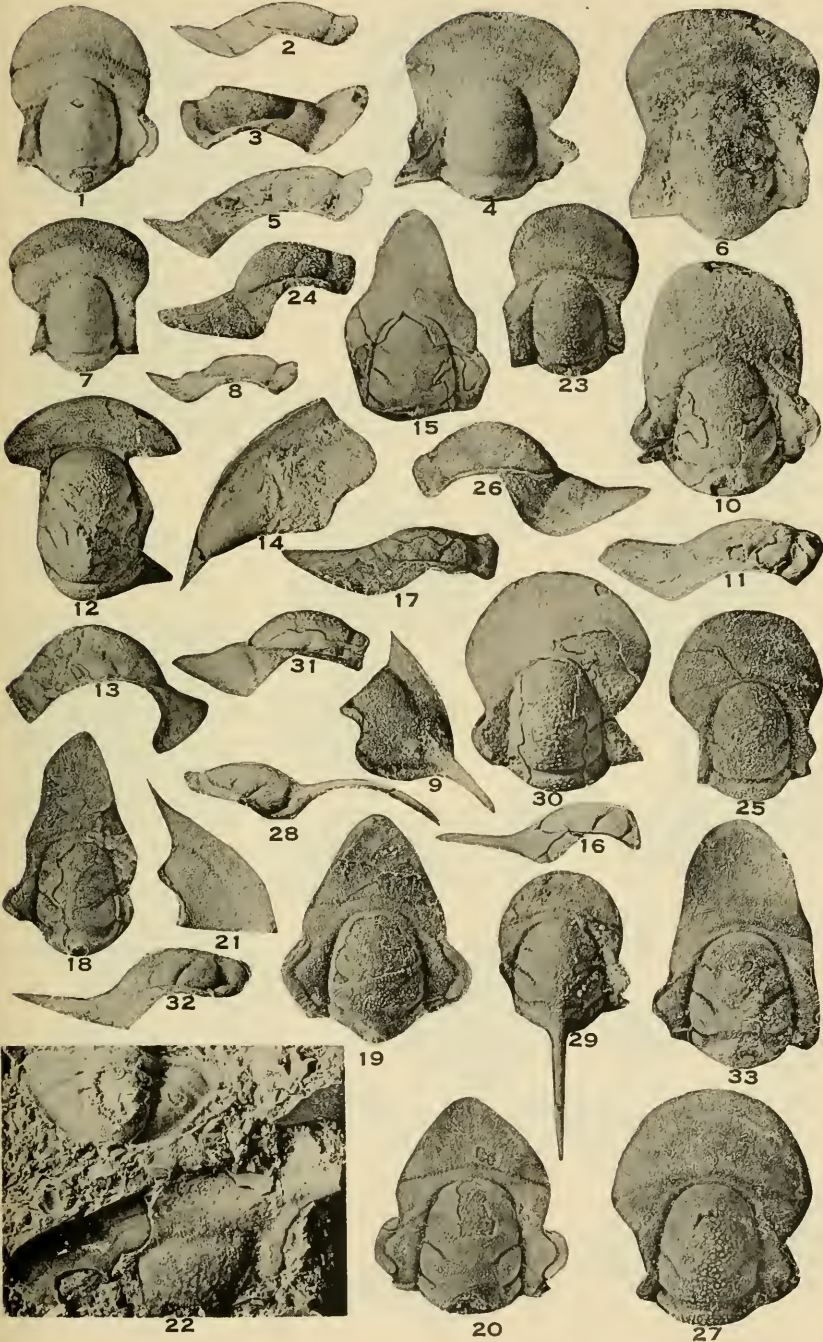
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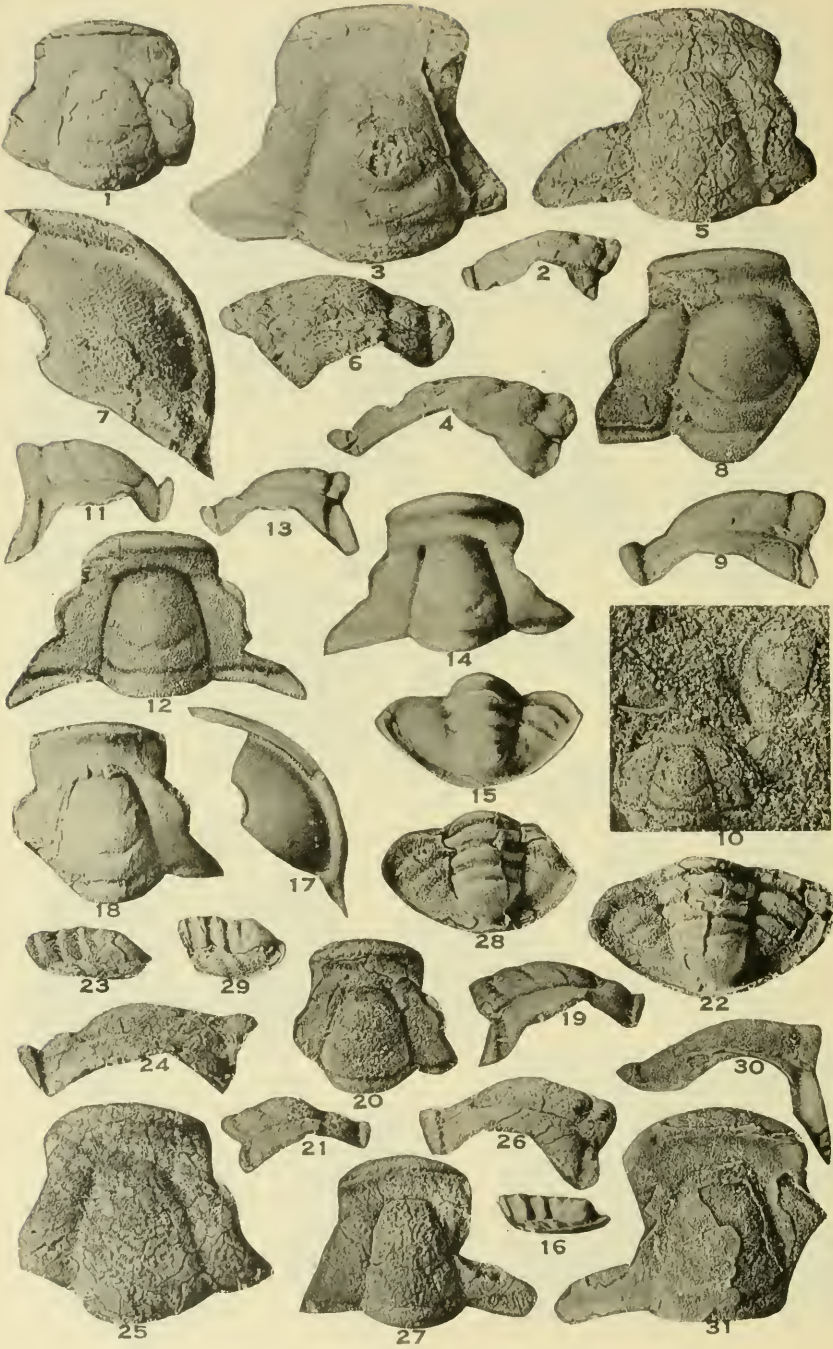
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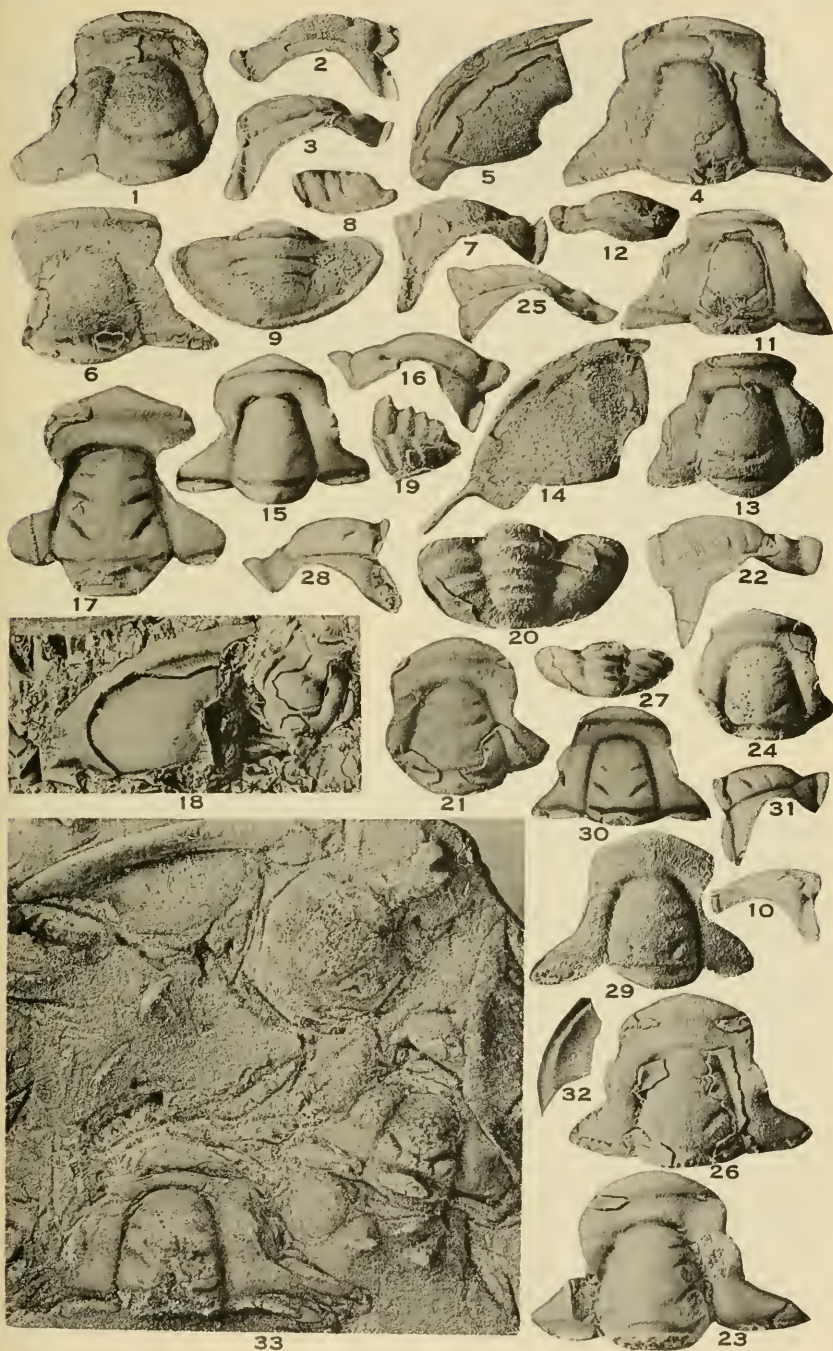


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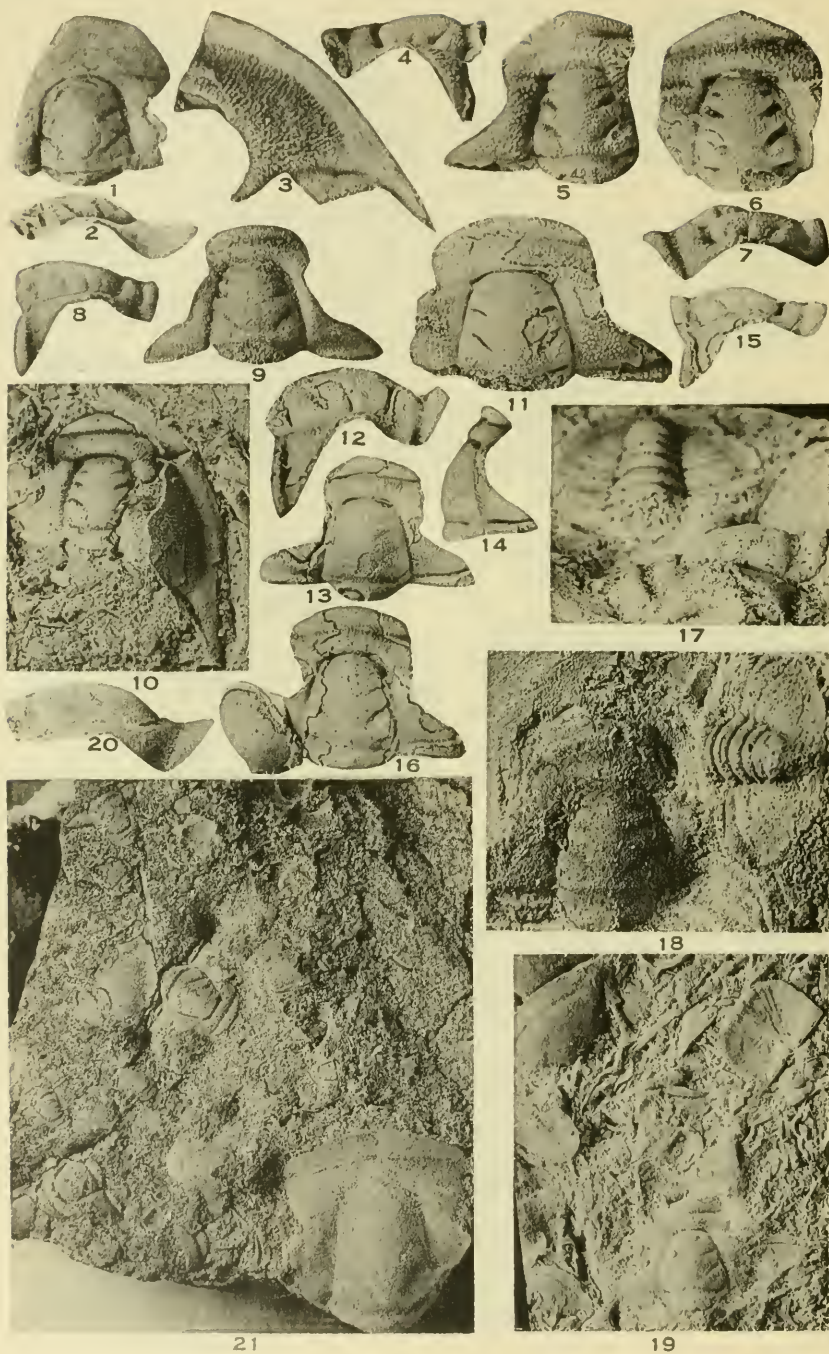
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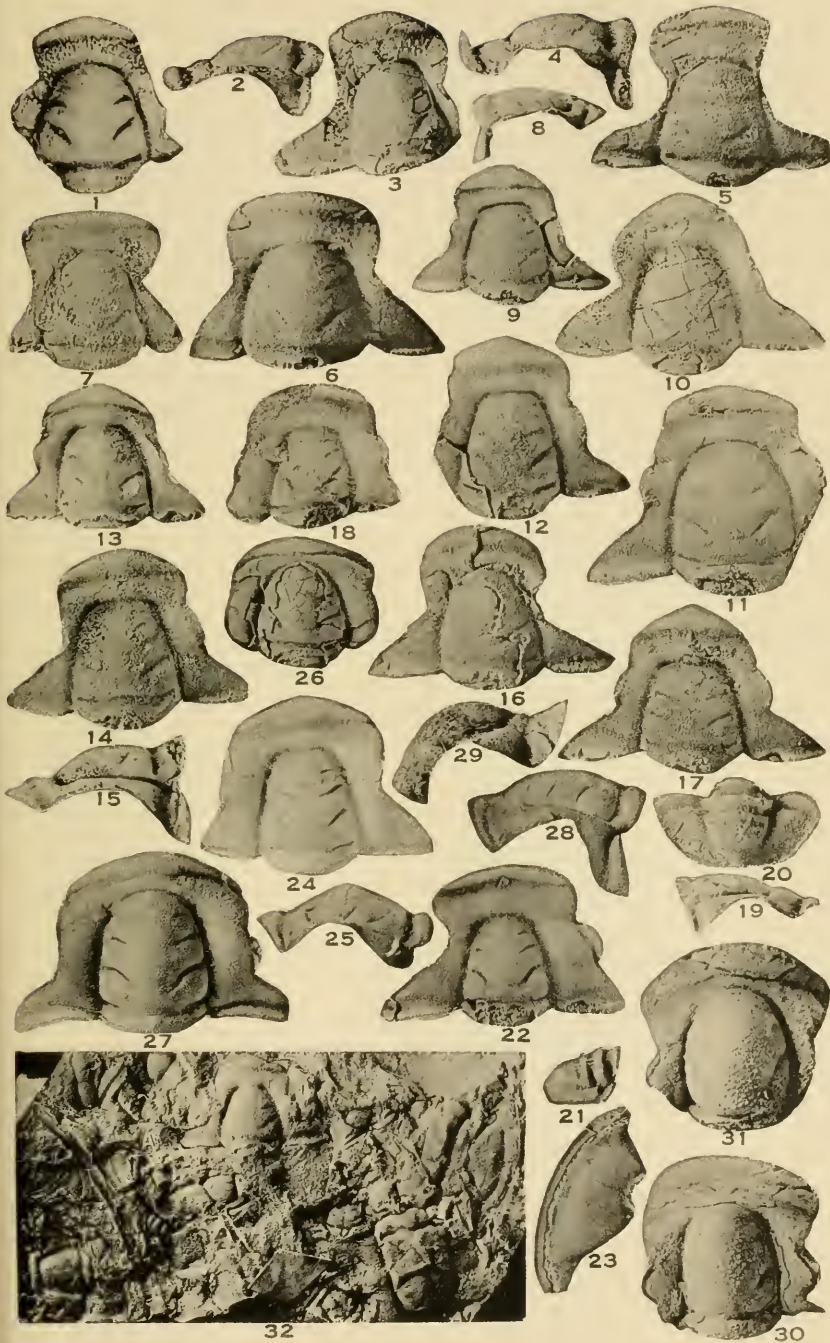
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SMITHSONIAN MISCELLANEOUS COLLECTIONS

VOLUME 103, NUMBER 6

ON THE PREPARATION AND PRESERVATION OF  
INSECTS, WITH PARTICULAR REFERENCE  
TO COLEOPTERA

BY

J. MANSON VALENTINE

Bureau of Entomology and Plant Quarantine

U. S. Department of Agriculture



(PUBLICATION 3696)

CITY OF WASHINGTON

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# ON THE PREPARATION AND PRESERVATION OF INSECTS, WITH PARTICULAR REFERENCE TO COLEOPTERA

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It is beyond the scope of the present paper even to enumerate the multiplicity of methods employed and customs adhered to in the preparation of insect specimens for the cabinet. Rather, what is intended is solely a presentation of certain procedures which have proved most useful to the writer after a period of considerable experimentation.

Broadly classified, there are two schools of technique in the mounting of Coleoptera. The European entomologist habitually displays his smaller specimens by gluing each of them, ventral surface down, to a standard rectangular card which is then pinned. The American prefers to mount his at the apices of small cardboard triangles whose bases hold the pins. In the first method, the appendages are protected but only the dorsal aspect of the insect is visible, an examination of its ventral characters necessitating the removal of the specimen from the card. This is a tedious and dangerous routine which the average collector is reluctant to undertake; its avoidance, however, cannot fail to result in identifications based entirely on dorsal anatomy. The American system, on the other hand, while providing opportunity to study lateral and ventral characters (though only those not obscured by the legs in their flexed positions) fails to afford proper protection to the specimen. Neither technique ordinarily includes any degreasing treatment with the result that too often, during the passage of time, escaping oils render the specimen unfit for study.

The following is a description of a third procedure which attempts to combine the merits of both schools and, at the same time, to eliminate the more undesirable features of each. This technique was developed specifically for the purpose of preparing good research material in the Cicindelidae and Carabidae. However, it has proved equally useful in other groups of beetles; and it has been adapted with success to insects of various additional orders, especially to those whose membranous wings, if present, are folded and concealed.

## I. KILLING

Since the final results are, in large measure, dependent upon the killing agent used, and the manner in which killing is accomplished, the choice of a suitable lethal chemical and its proper application become matters of the highest importance. In general it may be said that killing by means of the vapors from volatile anesthetics (lipoid solvents) is to be preferred to direct submergence in any fluid. Two such substances are recommended:

*a. Carbon tetrachloride.*—If specimens do not come into direct contact with the fluid, they will remain relaxed after death, especially if the catch is large and is allowed to remain in the killing bottle at least 24 hours. A full bottle, however, should not be neglected longer, as disintegration of soft parts will soon set in with consequent loss of setae and abdominal segments. A convenient vehicle for carbon tetrachloride is chopped elastic bands; rubber imbibes the fluid readily and retains it a long time. Crumpled paper toweling is also satisfactory, especially when used in connection with light traps requiring the efficient operation of large killing jars at least partly open to the outside air. The heavy fumes arising from a paper towel saturated with carbon tetrachloride will seek the bottom of the jar, which will remain lethal throughout the night.

## Advantages:

1. Produces fair to good relaxation. In this respect it is better than either cyanide or alcohol.
2. Assists in the extraction of oils and fats.
3. Prepares the specimen for genitalic examination by causing excessive swelling when subsequently dropped into ether, an event usually resulting in the extrusion of the genital apparatus.

*b. Ethyl acetate (acetic ether).*—For all general purposes, this is an ideal killing agent. Its advantages when used as such were first pointed out to the author by Prof. Candido Bolivar, whose technique was to half fill a collecting tube with coarsely ground cork moistened (not wet to the point of adhesion) with the ether. Strips of paper or pieces of cotton tape moistened with ethyl acetate and placed in a vial are equally effective and are better for very small specimens. A still more efficient method is to introduce a half inch or so of wet, mixed plaster of paris in the bottom of a tube or vial. Allow the plaster to set; dry it thoroughly in an oven; then saturate it with ethyl acetate, pouring off any excess fluid after complete impregnation. A collecting bottle of this sort may "stand up" under months of use, if not left uncorked. When exhausted, it can be dried again in the oven and recharged with ethyl acetate. It is advisable to allow

the day's catch to remain in the killing bottle at least overnight, in order to insure the maximum relaxing effect of the vapor-filled atmosphere. Insects may thus be preserved, while awaiting mounting, for an indefinite period, especially if they receive an occasional wetting of ethyl acetate. It is better, however, to remove them for drying, degreasing (II), or preserving in fluid (X) before many weeks have passed.

Advantages:

1. Specimens killed by the fumes of ethyl acetate are completely relaxed and retain their flexibility when subsequently degreased in ether (II) or preserved in Barber's fluid (X). Success in mounting such material on a flat, smooth surface, or in arranging appendages after direct pinning, or in relaxing specimens that have dried is far greater than when either cyanide or alcohol has been used as the killing agent.

2. Unlike the average cyanide jar, an ethyl acetate-charged killing bottle acts promptly, permanently, and uniformly over a considerable period of time. Insects show no tendency to revive if they are allowed to remain in the lethal atmosphere a few minutes after all motion has ceased, and delicate Lepidoptera as well as powerfully jawed beetles usually succumb before they can injure themselves or other specimens in the same bottle.

3. No fading or discoloration has so far been observed by the author as a result of killing beetles and their larvae with ethyl acetate. However, the green pigment of certain moths may turn yellow if the specimens are not removed from the killing bottle as soon as dead.

4. The use of ethyl acetate presents no such hazard as does cyanide, which is far more toxic to human beings.

5. Ethyl acetate is an ingredient of the relaxing fluid described below (XI) and a solvent for cellulose cement; hence its use as a killing agent simplifies the field technique by reducing the number of necessary fluids to be carried on a trip of long duration.

## II. DEGREASING

The use of some lipoid solvent in the preparation of Coleoptera, especially carabid, cicindelid, and scarabaeid material, is of the greatest importance. Ordinary sulfuric ether<sup>1</sup> (the commercial product) suffices very well. Specimens should be soaked in ether until the

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<sup>1</sup> Ether can be conveniently and economically stored in 1-pound cans fitted with small screw caps seated with cork. While in use as a grease solvent, it will keep well in tightly corked homeopathic vials.

fluid ceases to grow yellow owing to dissolved oils, one or two changes of the bath aiding the process when the bulk of material is great. The duration of treatment varies from about 12 hours to a week, depending upon the size and number of specimens per bottle, the volume of ether in proportion to material, and the fat content of the particular insects being degreased. To protect the specimens from the clinging, watery exudate which escapes from them and tends to work its way to the bottom of the container, a small wad of loosely folded absorbent tissue or filter paper should first be placed in the bottle. This will serve to capture such waste.

Ether will preserve ethyl acetate-killed material in a perfectly relaxed condition for an indefinite period. However, a certain degree of surface etching will take place in very oily ether where specimens should never be left very long. Also, very small specimens isolated in a volume of ether too large to be discolored by them may become temporarily brittle if given this treatment for more than a few hours. Should such an event occur, a drop of Barber's fluid (XI) on the dry insect will serve to free its articulations instantly.

Bulky specimens which have swelled in the ether bath should be removed to a pad of absorbent paper where all turgidity can be eliminated by gentle pressure after pricking through the dorsal abdominal and nuchal membranes with a needle. Such material should always be returned to clean ether for further degreasing before mounting.

Very hairy insects<sup>2</sup> and those possessing easily detached scales or farinose areas should be subjected to the ether bath only when the oily nature of the species at hand demands such treatment. Relatively few Coleoptera (certain groups of farinigerous Buprestidae, Curculionidae, etc.) fall under this category. These cannot be ether-treated for long without the loss of at least some of their powdery secretion.

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<sup>2</sup> Degreasing of pilose insects, such as some bees, flies, etc., must be thorough if attempted at all. When body fats have been completely removed, the pile may rather easily be restored to its natural fluffiness by lifting it with a camel's-hair brush while applying a stream of air through a blowpipe. The detachable pile which covers the bodies of moths cannot, of course, withstand rubbing or brushing. Gravid females of large-bodied species, however, often require degreasing because of the high lipoid content of their egg masses: since immersion is to be avoided in such cases, it is therefore desirable, before spreading these, to remove the viscera through an incision in the ventral abdominal wall. By clamping the pin (head end) in a horizontal position, it is possible to perform this operation with the abdomen hanging free. The abdominal cavity should be dusted with cotton dipped in dry plaster, blown clean, and loosely stuffed with fresh cotton.

Advantages:

1. Ether effects the extraction of body fluids as well as complete degreasing. After the ether bath, piceous, castaneous, and fulvous specimens will acquire a remarkable freshness of color, lightly pigmented areas appearing in vivid contrast to dark as soon as evaporation has taken place. Likewise, the true texture of the chitin, a useful habitus character dependent upon clean microsculpture, will be preserved as in life.

2. Never soiled with a sticky layer of grease to which dust and fine litter adhere, the ether-treated specimen can always be cleaned with a dry camel's-hair brush with minimum danger to setae.

3. The greaseless insect can be firmly cemented to the mounting support; should it become dislodged, its lightness and flexibility will insure a good chance of survival intact. Specimens exuding grease after they have been mounted on points or cards invariably discolor the paper and not infrequently work loose; when pinned directly, they usually corrode their pins.

4. Ether-treated specimens acquire atmospheric moisture rapidly and never become brittle under ordinary climatic conditions. In this respect they contrast very favorably with grease-soaked specimens whose ligaments and musculature eventually harden.

5. Swelling is accomplished by means of the ether bath, specimens killed with the fumes of carbon tetrachloride becoming so turgid in ether that usually the aedeagus and frequently its internal sac are extruded (III). This may be a great advantage, insofar at least as small carabids are concerned, since it eliminates the difficult process of dissecting such material. The more moderate distention of ethyl acetate-killed specimens in ether is useful not only in the extraction of genitalia, but also in the preparation of soft-bodied larvae (IX). Soaking in ether, however, will not cause swelling or extrusion of genitalia in previously dried material.

There are, of course, other satisfactory, though perhaps not equally efficient, lipid solvents which may be used in place of ether. Chloroform, benzol (benzene), and diethyl carbonate all yield good results but tend neither to be imbibed nor to expel body fluids so readily. Xylol (xylene) is pleasant and convenient to use, but its tendency to stiffen articulations and to deposit a whitish film are disadvantages. Chloroform is the only one of these solvents heavy enough to float both the specimens and their extracted body fluids, a fact which makes it desirable to separate the two with a wire screen. Ether, on the other hand, being lightest of all, permits both to sink, while diethyl carbonate, xylol, and benzol effect a more or less temporary



separation, the water alone, at first, falling to the bottom. Of the three last named, diethyl carbonate is the most efficient solvent. It is less volatile than ether and therefore safer to handle.

### III. STEPS PREPARATORY TO MOUNTING

When thoroughly degreased and ready for mounting, specimens should be removed from the ether bath to a pad of absorbent tissue, where, if desired, jaws may be separated and genital extrusions completed. Carabid jaws may best be opened by springing them apart by means of fine forceps applied ventrally. Provided the killing technique has been followed as indicated, the jaws will yield readily and the disclosed mouth parts may then be easily cleaned with a soft camel's-hair brush dipped in ether. Partial extrusion of the genital apparatus of males may be successfully completed by slight pressure on the abdomen; should this not produce the desired result, the insect is placed ventral surface uppermost and held while a sharp needle is inserted in a membranous portion of the median lobe and the latter gently extracted. The laterally curved aedeagi of carabids require urging counterclockwise in the direction of their curvature. Any fluids escaping from the body during the process of handling should be washed off in a bath of clean ether. If the specimen is minute, the operation should be performed in fluid (ether or Barber's fluid) under a binocular, a special tool of fine pin wire or drawn glass holding the beetle firmly against the bottom of the dissecting dish (fig. 1).

It is desirable to transfer drying specimens to a smooth, clean surface (preferably glass) for the final arrangement of their appendages. In preparation for the slip method of mounting, the legs are oriented close to and on a plane with the body, and the antennae are directed backward along the sides. Until cleared mounts of genitalia are desired, these organs had best be left attached to the abdomen; in male Carabidae and Cicindelidae, they tend to orient pointing clockwise as seen from above and in this position they are most convenient for study.

### IV. MOUNTING ON TRANSPARENT SLIPS

A sufficient series of each species collected at one time and under the same ecological conditions are assembled and are ready for mounting as soon as their surfaces are dry. Mounting should be done before the insects have become stiff, since the legs in drying tend to elevate the body slightly and this necessitates relaxing the specimens again before they can be properly cemented to a plane

surface. Should this eventuality arise, the dried insects can be completely and instantaneously relaxed merely by dipping them in Barber's fluid (XI).

The foregoing technique is preliminary to mounting on a transparent supporting surface, though it does not preclude pinning in the usual manner. The former, or slip system, applicable to large specimens as well as small, has been developed in two ways:

*a. Cellulose acetate mounting.*—Only the best quality, heavy (.015, .020, .025 inch = 15, 20, 25 gauge) acetate sheeting<sup>3</sup> can be used to

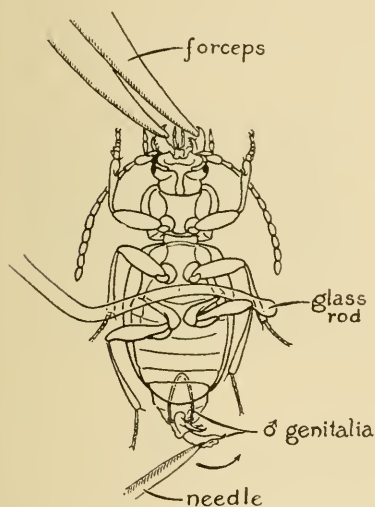


Fig. 1

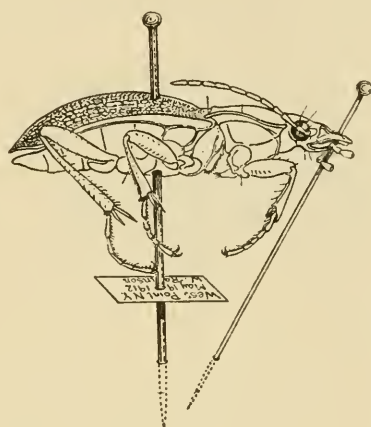


Fig. 2

FIG. 1.—Preparing a minute male carabid for mounting.  
FIG. 2.—Preferred arrangement of parts in a pinned carabid.

advantage. This material, unlike celluloid, will not curl when pinned nor, apparently, will it discolor or lose any of its transparency when exposed to the light. Up to 25 gauge, it can be cut easily with ordinary scissors, can be punctured with a No. 3 pin, and will grip the latter firmly without need of reinforcement.

On a piece of acetate sheeting of convenient size and gauge, each species-time-locality series is cemented separately in a compact group, usually of one row. Adequate space is left between the groups so

<sup>3</sup> Acetate sheeting ordinarily tends to fog by collecting droplets of an oily fluid when in contact with the fumes of pest and mold repellents such as naphthalene, paradichlorbenzene, phenol, creosote, etc. Carbon tetrachloride, however, has no such effect on it. Sheeting which will *not* fog under the above conditions can be obtained from Eastman Kodak Company, Rochester, N. Y.

that they may be cut apart without danger to appendages; and an ample margin of free sheeting should remain in back of each group in order that the pin, which is placed there, may not interfere with hand-lens observations of the specimens nearest it (fig. 3). Standard strips of 15-gauge sheeting cut in  $\frac{1}{2}$ - and  $\frac{3}{8}$ -inch (13-mm. and 10-mm.) widths will greatly facilitate the mounting of small to minute specimens and will lend a neat appearance to the collection. The beetles should face and be close to a long edge; the slips bearing series or single specimens can then be speedily cut apart in one operation yielding mounts of uniform dimension from back to front with the specimens thereon occupying similar relative positions. If sufficiently heavy sheeting is used for large beetles, it is seldom necessary to

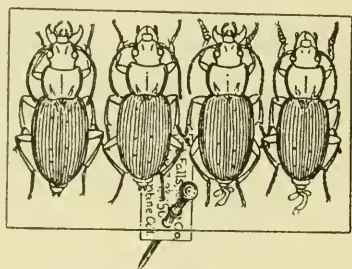


Fig. 3

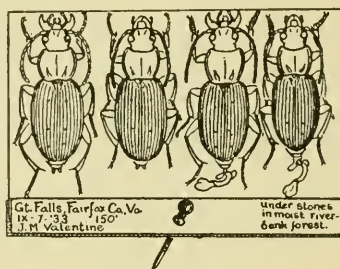


Fig. 4

FIG. 3.—The cellulose acetate slip method of mounting in series.

FIG. 4.—The cover glass slip method of mounting in series.

place the pin in any position other than the standard one, in the center of the rear of the mount. Should, however, an extra large mount require reinforcement, a drop of cement placed at the point of exit of the pin will suffice.

A good-quality, clear cement of cellulose base<sup>4</sup> should be used. It should not be applied straight from the container, however, but should first be diluted with sufficient solvent to allow small drops to form slowly on the head of a pin after the mixture has been thoroughly stirred. At least two lots should be made up, one diluted with ethyl acetate and the other with amyl acetate. The former is relatively quick-drying and is used in cementing firmly all but the smallest specimens to their acetate mounts; the latter is slower to dry and therefore more useful in attaching minute specimens and in mending broken appendages. A convenient applicator is the head of a long, fine insect pin stuck into the cork of the vial in which

<sup>4</sup> Duco "household" cement has been found very serviceable.

the cement is mixed. Good adhesion with a minimum droplet of cement depends, of course, upon the consistency of the latter, which should not be so thick as to provide poor capillarity, nor so thin as to spread beyond the original confines of the droplet.

Advantages:

1. An assemblage of specimens illustrative of a circumscribed population or of an ecological sample of a species provides far more valuable data than isolated specimens and should be kept intact under the same label. The slip method of mounting makes this possible for large specimens as well as small, and promotes comparison of individuals.

2. Too often the customary procedure of mounting small, flexed insects on cardboard points results in specimens whose appendages and ventral anatomy are seriously obscured by the adhesive. Another handicap to study frequently arises from undue arching of the body and depressing of the head. The transparent-slip technique allows maximum visibility of all parts, which, in all but the most convex forms (some weevils, mordellids, etc.), can easily be arranged so as to appear nearly on one plane. Under these conditions, buccal and appendicular anatomy and comparative dimensions of legs, etc., can be observed with a maximum degree of ease.

3. One of the commonest causes of damage in a collection is the inadvertent contact between protruding labels and specimens delicately mounted on points. The slip method obviates this hazard.

4. Mutilation of specimens and interference with hand-lens examination by pins thrust through elytra are eliminated.

5. Labels under acetate mounts are readable from above; usually they can be larger than the minimum-sized label customarily attached to specimens mounted individually.

6. A great saving of time is effected when specimens are mounted in series by reducing the number of labels necessary and speeding up transfer.

7. Space is conserved through the close approximation of specimens on the mounting slip.

8. Far fewer pins are used.

9. The problem of which method of mounting—pin or point—should be applied to a rather small specimen is eliminated; this makes for uniformity in the collection.

10. Any specimen can instantly be removed from the acetate mount merely by touching it with a brush containing ethyl acetate.

*b. Cover-glass mounting.*—This is a refinement of the above technique, micro cover glass (No. 1 or No. 2) being used in place of

acetate sheeting. Cover glass is best cut with a diamond point; a small chip cemented to the end of a drawn-glass tube makes a perfect instrument for the purpose. The slip may be cut to the required size after the specimen or series has been attached to it. It is imperative to work on a perfectly smooth, level surface, preferably plate glass; and to use a rule which will not slip, such as a microscope slide faced on one side with adhesive tape. The best adhesive for mounting on glass is acetate cement thinned with ethyl acetate. A generous application of a slightly thicker mixture should be used to attach two narrow strips of bond paper or single-ply bristol board (about  $\frac{1}{8}$  inch wide for small slips), one on each side of the glass along the entire rear margin of the mount. Approximately half the width of these strips should be occupied by the glass between them, the other half being left for direct contact of the strips and subsequent perforation by the mounting pin. The strips should be gently pressed together and carefully aligned. When working with a quantity of material of fairly uniform size, a number of slips can be attached at intervals to a long bottom strip, and a top strip of equal width can then be cemented over the whole. After 15 minutes or so of drying, before the cement has become thoroughly hardened, the mounts should be cut apart, the paper trimmed close to the glass with fine scissors, and each mount carefully pinned on a flat-topped, gauged block, preferably slotted (VI) (fig. 4). It is advisable to pin the mount tilted slightly upward, and to immobilize it with a drop of cement deposited on the bottom strip around the pin.

A well-constructed cover-glass mount is neat, strong, and optically ideal. However, unless its specimens have been exceedingly thoroughly degreased, it may, in time, collect fine droplets of oil emanating from them. Cover glass is, therefore, best employed in mounting small specimens (10 mm. or less) which can easily be cleaned of all grease.

The writer has experimented with a variety of materials for the supporting strips of these mounts. None of the transparent "plastics" and celluloids used has proved so efficient as heavy paper. Besides its stability, another advantage in the paper base is that it can effectively serve to display data, numbers, etc., written thereon.

#### V. DIRECT PINNING

Provided specimens are of sufficient size to justify impaling them on insect pins, they can always be effectively mounted in accordance with this standard technique. It should be pointed out, however, that substituting direct pinning in the larger forms for the transparent-



slip method entails some sacrifice of utility, safety, and uniformity. On the other hand, an obvious advantage in pinning lies in the resulting mobility of individual specimens. Whichever method is chosen, the quality of the finished product depends, to a large extent, upon two factors: proper killing (I) and adequate degreasing (II).

In mounting Coleoptera, the location of the pin is internationally agreed upon: It should enter the anterior discal portion of the right elytron and emerge on the right side between the mid and hind legs, passing through the metasternum laterad of the mid line; it should be so oriented that both longitudinal and transverse axes of the beetle are at right angles to it. The writer recommends the European system of appendage arrangement as combining neatness and compactness with maximum visibility. The head and pronotum are extended, with antennae close to the dorsal surface and directed straight back; the legs are directed downward and toward the pin, but with femora more or less horizontal and close to the body, the anterior femora pointing forward, the mid and hind pairs pointing backward. A fresh specimen naturally assumes this attitude when pinched laterally between the fingers. If the insect has been killed with ethyl acetate, its appendages will usually dry in position without the necessity of guard pins. However, drooping of the head and pronotum may occur. This can be remedied easily by resting the jaws (open if possible) of the drying specimen on an outwardly inclined pin placed before it (fig. 2).

## VI. GAUGING

Mounting specimens at an approximately uniform height not only makes for neatness in the collection but facilitates microscopic comparisons. Two or three standard heights should be decided upon as proper for corresponding categories of beetles of different body depths, and a gauge constructed which will automatically elevate the mounting support to the desired distance on the pin.

A glass-topped, slotted pinning block greatly facilitates both pinning and gauging. It can easily be constructed of plaster in a mold slightly larger (about  $\frac{1}{2}$  inch on each side) than the future glass working surface. The latter is composed of two pieces of plate glass, each 3 inches square, aligned along one edge but held slightly apart by two narrow strips cut from the ends of a microscope slide, inserted in the slot between the plates at the corners, and cemented there in an upright position. The thickness of these lateral pieces should gauge the width of the slot just to accommodate the shaft of a No. 5 insect pin. Two microscope slides are then placed at right

angles with the top plates, flush with and on each side of the slot and contiguous with the lateral pieces to which they are cemented. The space between the slides from the ends of the lateral pieces to the longitudinal free margins of the slides (a distance equal to the thickness of the top plates) is filled by a strip of appropriate width cut the full length of a slide and cemented in place to form the floor of the slot. If preferred, a strip of hard wood, to cushion the points of the pins, may be substituted here for glass. The slot depth, from the free surface of the top plates to the inner edge of the bottom strip, now measures the width of a microscope slide (about 1 inch)

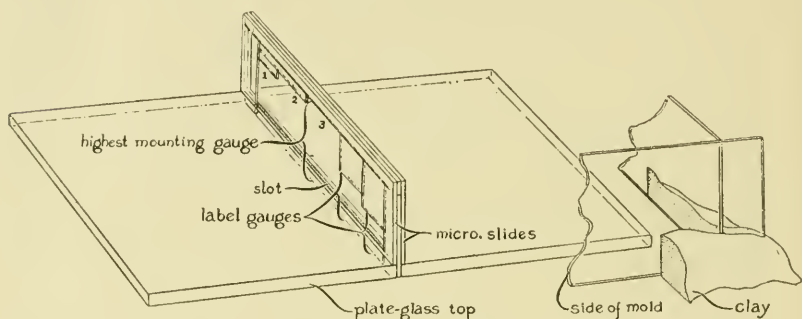


Fig. 5

A slotted pinning block in process of construction.

and gauges the correct position for slips bearing medium to small beetles on the standard 34-mm. ( $1\frac{3}{8}$ -inch) pin. Additional gauges for lower levels of the mounting slip, as well as for pin-label heights, may be had simply by inserting small removable glass rectangles of the proper widths at the ends of the slots, an operation which had best be performed after the block is otherwise completed. The glass assemblage is now placed, top downward, in the center of the mold and mixed plaster of paris poured over it to a depth greater than the walls of the slot (fig. 5).

A slotted pinning block makes it possible to pin mounting slips squarely with reference to the transverse axis, yet with the longitudinal axis at a slight angle to the horizontal. It is advisable, when pinning heavy mounts, to tilt them slightly upward in front in order to compensate for gravity, and to strengthen them by means of a drop of cement placed so as to embrace the pin at its point of exit.

## VII. LABELING

There exists an established precedent of long standing that pin labels, when oriented parallel to the specimen, should face to the right. This custom originated at a time when hand-lens observations were the rule; its function was to insure legibility of labels when specimens were examined in the left hand, the right remaining free for manipulation of the lens. Since the binocular dissecting microscope has come into almost universal usage in entomology and the lifting of specimens with the right hand is, ordinarily, the safer procedure, it follows that a system which would permit labels on specimens held in the right hand to be read without rotating them is to be preferred. Consequently, the writer recommends pinning labels for slip mounts through the right end so that the printing will face left. Additional reasons for this procedure are these: There is usually a pinning space in the uneven right-hand margin of a label; and also, any identification label thus oriented may, when desired, be swung into the standard, left-hand position without becoming inverted. Labels on specimens pinned individually, without mounting support, had best be pierced through the center and oriented facing left, parallel to the specimen.

Double-ply Reynolds bristol board or single-ply Strathmore makes an admirable label paper of the proper thickness to grip the pin effectively. Should a label work loose, a drop of acetate cement on the under surface around the pin will serve to fasten it securely.

## VIII. MOUNTING DISSECTIONS

Preparations of mouth parts, legs, genitalia, etc., may be attached dry to the mount bearing the specimens which yielded them. Should a transparent preparation be required, the subject, partly dried on absorbent paper, can be both cleared and dehydrated in xylol, and from this transferred directly to a drop of balsam on the glass or acetate mounting slip close to the specimen to which it belongs. After proper orientation of the dissection by means of a needle, a tiny square of cover glass, or thin acetate sheeting (7.5 gauge), is placed over it. Another method, useful in attaching cleared preparations to specimens mounted individually, is to prepare a small balsam mount on one end of a rectangle of acetate sheeting and run the pin through the opposite end. When not being examined, such a mount may be swung out of the way under the specimen.

Bulkier genitalia, which require examination in more than one plane, may be conveniently prepared for study as cleared objects

by placing them (after dehydration in strong alcohol and clearing in xylol) in small sections of glass tubing drawn to an appropriate gauge and filled with balsam or, better still, with a color-stable gum damar. One end of the tube is left open for addition of more mounting medium as contraction takes place; the other end is closed with a tiny cork plug, or by embedding it in a small cork block in which a suitable recess has been cut with a cork borer. Through the free end of the cork is thrust the pin of the specimen which yielded the dissection. The tube should eventually be sealed with thick acetate cement. Examination of its contents should be made in xylol or cedar oil, where virtually all optical interference due to the curved glass will be eliminated.

The presence of small air pockets trapped within or adjacent to a dissection in a freshly made balsam mount need not be viewed with concern; after a few hours, these will disappear.

#### IX. MOUNTING LARVAE

Soft-bodied forms, especially the larvae of Coleoptera, have been successfully treated exactly as the adults and mounted with them on the same slips. There is but one departure in technique: While drying, after having been thoroughly soaked in ether, the specimen is warmed under an electric lamp sufficiently to cause expansion of the gas within its body and consequent distention. The heat must be carefully applied and maintained for a few minutes until the specimen has dried in an inflated condition. Too sudden an increase in heat will cause rupture, too gentle an application will cause collapse of the body.<sup>5</sup>

#### X. CARE OF ACCESSORY MATERIAL

*a. Dry storage.*—The flat tin boxes in which 50 cigarettes are sold provide admirable storage facilities for Coleoptera. They may be made to do double duty if both top and bottom are utilized. After the metal is first scored with a sharp instrument, two pieces of heavy, smooth cardboard are attached, one to each of the inner surfaces, by means of a suitable cement (such as "Metallic X"). To these cards the ethyl acetate-killed, ether-treated specimens are cemented in close array, with legs at the sides and antennae pointing backward. This should be done while the beetles are still relaxed, and the ad-

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<sup>5</sup> This method has yielded excellent results in the preparation of degreased and dehydrated lepidopterous larvae of both smooth and hairy species.

hesive employed should be acetate cement, somewhat diluted with ethyl acetate. Each lot, representing a day's catch or an ecological aggregate, is circumscribed with an ink line and labeled with the date and locality, or with the date plus some symbol referring to a category in the chronologically arranged notes. The boxes are stored chronologically in cardboard filing cases (12 by 6½ by 5 inches), where they stand vertically, hinge uppermost, each bearing an adhesive-tape label along its upper edge. If the cementing has been carefully done and the specimens are clean, the chances of their breaking loose, even in shipping, are extremely remote. Space for naphthalene on the bottom of the filing case is provided by the recess in which the filing mechanism operates. However, should dermestids succeed in entering the tin boxes, they can be destroyed without disturbing the contents simply by dousing specimens and all with carbon tetrachloride and shutting the lids for a few hours.

The chief advantages gained by the above technique lie in the visibility of the specimens and in the compactness of their arrangement. If at any time a beetle is required for mounting, it may be detached immediately from the cardboard after an application, by brush or pipette, of ethyl acetate. It should then be immersed in the relaxing bath (XI) where any residual cement will be dissolved.

*b. Preservation in fluid.*—Adequate preservation of soft parts with minimum hardening of tissues and stiffening of joints are the criteria for a good entomological preservative. In the writer's opinion, Barber's relaxing mixture (XI) meets these requirements better than any preservative in common use. Ethyl acetate-killed material, stored in this fluid either before or after ether treatment, has emerged years later in an excellent state of preservation and perfectly relaxed. It has proved particularly useful as a preservative or softener for carabid beetles captured in molasses traps, the specimens being soaked in the fluid after having been thoroughly washed and partly dried. In using Barber's fluid as a preservative over a long period of time, it is important to remember to change the supply as often as it becomes darkened by dissolved oils. When the bulk of material is great, several changes may be required.

Because of their hardening properties, neither alcohol nor formalin should be employed alone as a preservative when flexibility of articulations is prerequisite to the mounting technique adopted. Furthermore, the use of these fluids in killing and preserving seems to inhibit, somewhat, the action of degreasing agents. However, the ease with which specimens can be collected and preserved in alcohol frequently justifies its use, especially when time, simplicity of method,



and quantity of material are considerations, or when a hard fixation of perishable internal organ systems is desired for purposes of dissection. If alcohol is used for preserving Coleoptera, strengths neither exceeding 70 percent nor less than 50 percent are recommended.

## XI. RELAXING

The writer has found the relaxing mixture developed at the United States National Museum by Herbert S. Barber to be extremely efficient and versatile. In this fluid, ethyl acetate-killed specimens become plastic almost instantly and genitalic dissections may be made a very short time after immersion. It is invaluable for rejuvenating old, greasy specimens, and will dissolve every mounting adhesive now in common use. The formula is quoted below:

### *Barber's fluid*

Ethyl alcohol (95 percent) .....	265 parts
Water .....	245 parts
Ethyl acetate (acetic ether) .....	95 parts
Benzol (benzene) .....	35 parts

Should the benzol separate out, a little alcohol, added slowly with shaking, will serve to bring it back into the mixture.

Relaxing alcohol-killed material preparatory to slip mounting presents a difficult problem. However, if such specimens are completely dried under a lamp, then slightly moistened with Barber's fluid and quickly blotted, recalcitrant appendages can usually be made to remain in the desired positions. A simpler and perhaps more efficient method consists in a thorough soaking (several hours at least) in chloroform. Articulations then become fairly easy to manage, especially in the smaller specimens whose appendages, while they are still moist, readily yield to manipulation with needles.

## ACKNOWLEDGMENTS

The author wishes to express his gratitude for the helpful suggestions and encouragement received throughout the course of this work from Edward A. Chapin, of the United States National Museum, and from Herbert S. Barber and L. L. Buchanan, of the Bureau of Entomology and Plant Quarantine, United States Department of Agriculture.





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VOLUME 103, NUMBER 7

THE MUSCULATURE OF THE LABRUM,  
LABIUM, AND PHARYNGEAL REGION  
OF ADULT AND IMMATURE  
COLEOPTERA

(WITH 24 PLATES)

BY

CARL KESTER DORSEY

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*Bureau of Entomology and Plant Quarantine, U. S. Department of Agriculture*

(WITH 24 PLATES)

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## INTRODUCTION

This paper presents the results of a comparative study of the muscle arrangement in certain regions of the insect head and stomodaeum. A preliminary study was made in Orthoptera, Dermaptera, Hymenoptera and Neuroptera, and was followed by a similar but more inclusive study of representatives of adult and immature stages of the order Coleoptera.

Several species of orthopteroid insects were dissected to determine the muscular arrangement in a generalized form of insect. The other orders are included to observe similarities with and variations from the type of muscle system in Orthoptera, of which *Periplaneta americana* L. is chosen as the most generalized form.

In order to observe carefully the places of origin and insertion of the labral, labial, hypopharyngeal, and pharyngeal muscles it is necessary to remove the maxillae and mandibles and their muscles. The maxillary, mandibular, and antennal muscles are not included in this study.

This particular work evolved from an interest as to how chewing insects actually accomplish the feat of getting the food into the true mouth, which, of course, is located in the posterior region of the cibarium. Much is known as to how these insects procure and chew their food, but the hypopharynx though tongue-like in position could not be very efficient in accomplishing the work done by the tongue of a vertebrate. In many insects the hypopharynx, for all practical purposes, can be considered to be absent; such insects also ingest food and thrive, so the hypopharynx alone cannot be responsible for the act of placing the food in the mouth from which point it can be swallowed.

It is difficult and often impossible to identify corresponding muscles on a functional basis. A muscle, for example, as found in one species may be an adductor while its homolog in another species is perhaps a retractor because of some slight change in the position of the point of insertion. For this reason the general application of functional names to insect muscles is limited; a careful study of each species individually is necessary to ascertain muscle functions.

It is hoped that the facts of the arrangement of muscles, and certain anatomical observations herein presented will contribute to a better understanding of the means of ingestion of food by chewing insects, and also of the homologies of muscles between orders of insects, or between families within an order.

The Leng system of classification as modified by Böving and Craighead (1930) is followed, and at least one family from each superfamily selected from which a genus is chosen for study. When possible the immature stage of the same genus is used. The species of Coleoptera included in this study are not considered as representative, necessarily, of their respective families.

This work is presented in partial fulfillment of the requirements for the degree of Doctor of Philosophy in the Graduate School, Entomology Department, University of Maryland. The study was carried on under the direct supervision of R. E. Snodgrass of the United States Department of Agriculture, Bureau of Entomology and Plant Quarantine, who is also a member of the staff of the University of Maryland, Entomology Department. The writer is sincerely grateful to Mr. Snodgrass for his guidance and encourage-



ment throughout this entire study, and also to Dr. Ernest N. Cory, head of the Entomology Department, University of Maryland, for his helpful criticisms. The assistance of the United States National Museum in the loan of certain immature stages of Coleoptera for study is appreciated as is also that of several specialists in the Division of Insect Identification, Bureau of Entomology and Plant Quarantine, for their help in the identification of certain species.

## I. GENERAL DISCUSSION OF THE MUSCULATURE

Among the orthopteroid insects there is apparently, with minor variations, a general plan of muscle arrangement. The American cockroach, *Periplaneta americana* L., is selected as a representative of Orthoptera exhibiting the generalized plan of musculature. The muscles included in this work are numbered for convenience of study and their homologies in other species and orders are considered.

The muscles are considered as occurring in definite pairs unless indicated as otherwise. The muscles in the dorsal region of the head inserted on the stomodaeum posterior to the paired nerve (frontal connective) that connects the frontal ganglion with the brain are considered as belonging properly to the frons; those muscles that are anterior to this nerve belong to the clypeal region proper.

1. *Compressor muscle of the labrum* (fig. 1).—An asymmetrical muscle arising in the posterior region of the dorsal wall of the labrum; inserted along the lateral margin of the ventral wall of the labrum.

2. *Dilator muscle group of the labrum* (figs. 1, 2).—A transverse band of fibers extending across the ventral wall of the labrum.

3. *Ventral (posterior) muscle of the labrum* (fig. 2).—Arises in the posterior region of the frons adjacent to the inner margin of the antennal rim and is inserted laterally at the base of the labrum on the torma.

4. *Dorsal (anterior) muscle of the labrum* (fig. 2).—Arises near the center in the posterior region of the frons and is inserted medially on the posterior dorsal margin of the labrum.

5, 6, and 7. *Dorsal dilator muscles of the cibarium* (figs. 1, 2).—Arise on the clypeal region slightly laterally and, with the exception of muscle 7, are inserted in the anterior region of the dorsal wall of the cibarium. Muscle 7 is inserted on the dorsal wall of the cibarium, midregion, between the transverse muscles, 12, of this area.

8. *Dorsal dilator muscle of the cibarium* (figs. 1, 1A, 2).—Arises centrally in the anterior clypeal region; it surrounds muscle 4 (fig. 1A) and extends ventrad to be inserted in the anterior region of the dorsal surface of the cibarium. This muscle was found only in *Periplaneta americana* L.

9. *Dorsal dilator muscle of the anterior region of the pharynx* (figs. 1, 2).—Arises on the frons anterior to muscle 11 and is inserted on the dorsal wall of the pharynx immediately behind the frontal ganglion connective.

10. *Muscle of hypopharyngeal bar Y* (figs. 1, 2).—A branched muscle: branch *a* arises on the frons immediately laterad of muscle 11 (fig. 1); branch *b* arises laterally in the anterior region of the frons. Both branches are inserted on the dorsal end of the sclerotized bar *Y* (fig. 1), branch *b* laterally.

11. *Dorsal dilator muscle of the pharynx* (figs. 1, 2).—Arises on the frons immediately laterad of the dorsal muscle of the labrum, 4, and is inserted slightly laterally on the dorsal wall of the pharynx.

12. *Compressor muscle group of the cibarium* (fig. 2).—Arises on one side of the dorsal wall of the cibarium, central region, and extends transversely across the surface to be attached on the opposite side.

13. *Compressor muscles of the anterior region of the cibarium* (fig. 2).—Arise laterally on the dorsal wall of the cibarium in the anterior region of muscle group 12; they extend diagonally anteriorly to be inserted on the dorsal surface of the cibarium mesad of one of the dorsal dilator muscles of the cibarium, 5.

14. *Hypopharyngeal muscle of the mandible* (fig. 1).—Arises on the lateral wall of the mandible and is inserted on the distal end of sclerite *X* (fig. 1). This muscle was found only in Orthoptera; it is, of course, common in apterygote insects and other arthropods.

15. *Anterior dorsal dilator muscle of the salivarium* (fig. 1).—Arises on sclerite *X* adjacent to muscle 16 and is inserted laterally on the ventral wall of the hypopharynx.

16. *Dorsal salivary cup muscle* (fig. 1).—Arises on the inner surface of sclerite *X* and is inserted, near the center, on the dorsal surface of the salivary cup.

17. *Anterior salivary cup muscle* (fig. 1).—Arises laterally on the ventral wall of the labium adjacent to the palpal base and is inserted laterally in the anterior region of the salivary cup anterior to muscle 18.

18. *Lateroventral salivary cup muscle* (fig. 1).—Arises laterally at the base of the prementum near the dorsal surface and is inserted laterally in the anterior region of the salivary cup.

19. *Muscle of the hypopharynx* (fig. 1).—Arises on the tentorial bridge immediately dorsad of muscle 20 and is inserted laterally on the base of the hypopharynx.

20. *Dorsal (anterior) muscle of the labium* (figs. 1, 3).—Arises on the tentorial bridge immediately dorsad of muscle 21 and is inserted laterally in the anterior region of the dorsal wall of the labium.

21. *Ventral (posterior) muscle of the labium* (figs. 1, 3).—Arises laterally on the tentorial bridge at the posterior end of the anterior tentorial arm and is inserted laterally on the base of the prementum.

22. *Muscle of the prementum* (figs. 1, 3).—Arises medially in the posterior region of the submentum and is inserted slightly laterally on the base of the prementum.

23. *Depressor muscle of the labial palpus* (figs. 1, 3).—Arises centrally on the dorsal wall of the labium at the base of the glossa and is inserted dorsally on the base of the palpus.

24. *Levator muscle of the labial palpus* (figs. 1, 3).—Arises laterally at the base of the prementum and is inserted posteriorly on the base of the labial palpus.

25. *Muscle of the labial palpus* (figs. 1, 3A).—Arises laterally on the prementum and is inserted basally and somewhat dorsally on the second palpal segment.

26. *Muscle of the labial palpus* (figs. 3, 3A).—Arises in the middle region of the ventral (posterior) wall of the first palpal segment and is inserted ventrally (posteriorly) in the middle region of the base of the third segment.

27. *Muscle of the labial palpus* (figs. 3, 3A).—Arises anteriorly at the base of the first palpal segment, inserted on the third segment basally on the anterior margin.

28. *Flexor muscle of the glossa* (fig. 3).—Arises medially at the base of the prementum and is inserted on the ventral wall of the labium at the base of the glossa.

29. *Flexor muscle of the paraglossa* (fig. 3).—Arises on the ventral wall of the labium at the base of the prementum and is inserted basally on the ventral wall of the paraglossa.

30. *Ventral dilator muscle of the pharynx* (fig. 1).—Arises on the tentorium and is inserted medially on the pharyngeal region just within the mouth.

31. *Lateral dilator muscles of the pharynx* (fig. 2).—Arise laterally on the dorsal head region adjacent to the inner margin of the compound eye posterior to the *muscle of hypopharyngeal bar Y*, 10, branch *A*, and are inserted on the side of the pharynx ventrad of the *dorsal dilator muscle of the pharynx*, 11 (fig. 1).

32. *Dorsal appressor muscle group of the cibarium* (fig. 2).—Arises on the dorsal pharyngeal surface posterior to the frontal ganglion and extends anteriorly beneath the *compressor muscle group of the cibarium*, 12, to be inserted on the dorsal wall of the cibarium adjacent to the anterior limits of muscle 12. These muscles are found in a well-developed state in the specimens used in this work only in Orthoptera, Dermaptera, and Neuroptera.

Two other Orthoptera were studied, the cricket *Gryllus assimilis* Fab. and the grasshopper *Melanoplus differentialis* (Thos.). In the latter there are no essential differences in the musculature. In *Gryllus* the muscle arrangement is practically the same as that found in *Periplaneta* except for a few minor variations; the *dilator muscle group of the labrum*, 2, is absent, the *ventral muscle of the labrum*, 3, is branched, and the *muscle of hypopharyngeal bar Y*, 10, is not branched.

As a representative of Dermaptera, *Anisolabis maritima* Gene was chosen (figs. 4, 5, 6). The *dorsal (anterior) muscle, 20, of the labium* (fig. 5), the *ventral (posterior) muscle, 21, of the labium* (fig. 5), and the *muscle of the prementum, 22* (figs. 5, 6), are essentially the same as those in *Periplaneta* except that muscle 20 arises posterior to muscle 21. The *muscle of the hypopharynx, 19* (figs. 5, 6), arises centrally in the middle region of the mentum instead of on the tentorial structure as it does in the cockroach; this is an unusual origin for this muscle, as it usually arises at some point on the posterior tentorial structure. The insertion of this muscle, however, does not vary. The *flexor muscle of the glossa, 28* (fig. 1), and the *depressor muscle of the labial palpus, 23* (fig. 1), are absent. The muscles of the labrum, cibarium, and hypopharynx are similar to those of *Periplaneta*.

In Neuroptera, *Corydalus cornutus* L. adult and larval stages were studied. The salivary muscles, in the adult form (figs. 8, 9), are similar to those of *Periplaneta*; the *anterior dorsal dilator muscle of the salivarium, 15* (fig. 1), is absent. The full complement of labial muscles is present. The *muscle of the hypopharynx, 19* (figs. 8, 9), arises laterally in the posterior region of the gula and is inserted at the base of the hypopharynx, but not on the sides of the salivary cup as is the case in *Periplaneta*. In addition to the usual *compressor muscle of the labrum, 1* (fig. 8), there is another muscle that arises immediately posterior to muscle 1 and is inserted in the anterior region of the cibarium on the dorsal wall; this muscle is probably only a division of muscle 1. The *ventral muscle of the labrum, 3*, and the *dorsal muscle of the labrum, 4* (fig. 8), are of the general form and arrangement. Of the *dorsal dilator muscles of the cibarium, 5, 6, 7* (fig. 8), muscle 5 is represented by a single pair of muscles; muscle 6 consists of two pairs, and muscle 7 is also made up of two groups of muscles on each side of the dorsum of the cibarium. The *dorsal dilator muscle of the anterior region of the pharynx, 9* (fig. 7), arises laterad of the *muscle of hypopharyngeal bar Y, 10*, instead of mesad which is the usual way.



In the larval stage of *Corydalus* (figs. 10, 11, 12) the muscles vary little from those of the adult, with a few exceptions and variations. Of the salivary muscles, 17 is absent. The *dorsal dilator muscles*, 5 and 7 (figs. 10, 12), are represented by a single pair of muscle groups. The ventral wall of the cibarium is furnished with well-developed transverse, longitudinal, and diagonal muscle groups (fig. 11, 33). These muscles were observed only in Neuroptera.

In Hymenoptera, *Sphecius speciosus* (Dru.) adults were selected for study (figs. 13, 14, 15, 16). This species possesses muscles that are massive and somewhat complicated in arrangement, and which are not easy to homologize with muscles of *Periplaneta*, though certain of them can be considered homologous. The *flexor muscle of the paraglossa*, 29 (fig. 13), arises basally on the ventral wall of the prementum and is inserted at the base of the paraglossa. There is present only one labial-palpus muscle, 24 (fig. 16); it is similar to that found in *Periplaneta*. The *dorsal salivary cup muscle*, 16 (fig. 13), arises on the inner surface of sclerite X (fig. 14) and is inserted laterally on the salivary cup. The *anterior salivary cup muscle*, 18 (figs. 13, 16), which arises immediately posterior to the *levator muscle of the labial palpus*, 24, on the ventral wall of the prementum, is inserted laterally in the anterior region of the salivary cup. The *muscle of the hypopharynx*, 19 (fig. 13), arises in the posterior region of the head and is inserted in the posterior region of the salivary cup immediately ventrad and caudad of the *dorsal salivary cup muscle*, 16. The *ventral muscle of the labium*, 21 (fig. 13), takes its origin on the inner side of the base of the anterior tentorial arm and is inserted centrally at the base of the prementum. The apparent *dorsal muscle of the labium*, 20A (fig. 13), arises on the anterior tentorial arm slightly above the *ventral muscle of the labium*, 21, and is inserted on the base of the cardo proximally, so it probably belongs to the maxilla and not to the labium. The *ventral muscle of the labrum*, 3 (figs. 14, 15), arises and is inserted in the usual manner. The *dorsal dilator muscles of the cibarium*, 5, 6, 7 (figs. 14, 15), are powerful and specialized. Muscle 5 arises centrally in the anterior region of the clypeus and is inserted centrally in the anterior region of the dorsal wall of the cibarium. Muscle 6 arises laterally in the anterior region of the clypeus adjacent to the clypeal suture and is inserted on the dorsal wall of the mid-region of the cibarium. Muscle 7 is posterior to muscle 6 in origin and insertion. The *compressor muscle group of the cibarium*, 12 (figs. 14, 15), is similar to that of *Periplaneta*. The specialized muscle 34 (figs. 14, 15) arises centrally on the dorsal surface of the modified bar Y (fig. 14) and



extends slightly diagonally and anteriorly to become inserted on the dorsal wall of the cibarium, anterior region; this is a compressor muscle of this region that may be homologous with the *compressor muscles of the anterior region of the cibarium*, 13 (fig. 2), in the cockroach. The two modified sclerites, bars *Y* (fig. 14), support the sides of the cibarium and stomodaeum; they are united by a continuously sclerotized area that strengthens the ventral wall of the stomodaeum. Muscle 34 (fig. 15) is inserted laterally on the distal end of the bar *Y*; this muscle extends laterally and anteriorly to its point of origin in the posterior region of the frons adjacent to the inner margin of the compound eye. The *dorsal dilator muscle of the pharynx*, 11 (figs. 14, 15), consists of a compact group of fibers and probably is a homolog of muscle 11 in orthopteroid forms. The *ventral dilator muscle of the pharynx*, 30 (fig. 14), is especially large and powerful; it arises on a sclerotized central projection from the anterior (dorsal) surface of the tentorial bridge by means of a tendon; it is inserted medially on the ventral surface of the continuous sclerotized area that supports the stomodaeum. This is a dilator muscle of the stomodaeum. It was thought on first examination that muscle 35 (figs. 14, 15) was homologous with the *muscle of hypopharyngeal bar Y*, 10 (fig. 1), in *Periplaneta*; this is not the case because the small frontal ganglion with its connectives lies posterior to this muscle, the function of which is not certain. In the honeybee, *Apis mellifera* L., there is a muscle which undoubtedly is homologous with the *muscle of the hypopharyngeal bar Y*, 10, found in *Periplaneta*; it consists of an anterior and a posterior branch inserted on the distal end of bar *Y*, and is posterior to the frontal connective nerve.

## II. MUSCLE ARRANGEMENT IN COLEOPTERA

The muscles of adult and immature Coleoptera included in this work are numbered as in *Periplaneta* and are considered to be homologous with those of the same designation in the orthopteroid forms unless indicated as being otherwise.

Certain muscles appear generally and consistently throughout the adult and immature stages in the order, though there are specialized muscles found in certain species and also generalized muscles that are greatly modified in size, shape, origin, and insertion. By considering the muscles of each superfamily separately it is easier to interpret homologies and the probable function of the various muscles.

## III. CARABOIDEA

In this group adult *Harpalus caliginosus* F., Carabidae (figs. 17, 18, 19), *Tetracha carolina* (L.), Cicindelidae, and *Laccophilus* sp., Dytiscidae, were selected for study. The labral muscles are absent in the three genera studied. In *Harpalus* the muscles of the cibarium 5, 6, and 7 (figs. 17, 19) and those of the dorsal and lateral pharyngeal regions are similar to those found in *Periplaneta*. Bar *Y* (fig. 19) is attached to a subpharyngeal brace. The *lateral dilator muscle of the pharynx*, 31 (fig. 19), is not considered, necessarily, as a homolog of 31 in *Periplaneta* or in any of the other species of Coleoptera since it varies greatly in size, form, and position; but the function being the same, it is given the same number. The place of origin of the labial and hypopharyngeal muscles is unusual. In the anterior region of the gula, caudad of the posterior tentorial pits there is a central invagination, or apodeme (fig. 19, *PTN*), which is finlike and of considerable size. The *muscle of the hypopharynx*, 19, the *dorsal and ventral muscles of the labium*, 20 and 21 respectively, and *muscle 21A* (fig. 19), arise on this apodeme and not on the tentorial structure as is the usual manner. It is possible that this apodeme represents a greatly modified tentorial bridge and tentorial arms. The *dorsal muscle of the labium*, 20 (figs. 18, 19), is inserted centrally on a projection that extends inward from the ventral labial wall in the basal region; it possibly performs the same function as muscle 20 in *Periplaneta*. *Muscle 21A* (figs. 18, 19) was found only in this species; it probably in some way supplements the action of the other labial muscles.

In *Tetracha* only the *dorsal and ventral muscles of the labium*, 20 and 21, respectively, and the *muscle of the prementum*, 22, are present; they arise centrally in the posterior gular region. The *dorsal dilator muscles of the cibarium*, 5, 6, and 7, are similar to those of *Harpalus*; the *compressor muscle group of the cibarium*, 12, is more strongly developed. The *dorsal dilator muscle of the pharynx*, 11, is powerfully developed. The tormae of the labrum extend posteriorly and then bend sharply ventrad to form a rigid lateral support on each side of the mouth; this rigid brace is continuous with the ventral head structure. Bar *Y* projects from the posterior dorsal region of this torma modification; the *muscle of hypopharyngeal bar Y*, 10, is inserted on its distal end.

In *Laccophilus* the *ventral muscle of the labium*, 21, originates in the posterior gular area. The *muscle of the hypopharynx*, 19, is single, broad, thin, and arises by means of a bifurcate tendon high on each anterior tentorial arm. The *compressor muscle group of the cibarium*,

12, is well developed. The *dorsal dilator muscles of the cibarium*, 5, 6, and 7, are essentially the same as those in *Harpalus*.

For the larval forms in this superfamily, *Amara* sp. and *Galerita* sp. were studied. In *Amara* (figs. 20, 21, 22) the *levator muscle of the labial palpus*, 24 (fig. 22), is strong and the *dorsal and ventral muscles of the labium*, 20 and 21 respectively, are large. The *dorsal dilator muscles of the cibarium*, 5, 6, and 7 (figs. 21, 22), are well developed. The pharynx is small; the *dorsal dilator muscle of the pharynx*, 11, is absent. Bar *Y* extends posteriorly along the sides of the cibarium and is connected with the one on the opposite side by a long, subpharyngeal, sclerotized area. In *Galerita* the *dorsal and ventral muscles of the labium*, 20 and 21 respectively, are similar to those in *Amara*. The *dorsal dilator muscles of the cibarium*, 5, 6, and 7, are grouped together to form a massive unit of muscle fibers. The *muscle of hypopharyngeal bar Y*, 10, is similar to that of *Amara*.

#### IV. GYRINOIDEA

The adults studied in this superfamily are *Dineutes discolor* Aubé and *D. vittatus* (Germ.), Gyrinidae. In *D. discolor* (figs. 23, 24, 25) the labral muscles are absent. The *dorsal dilator muscles of the cibarium*, 5, 6, and 7, the *dorsal dilator muscle of the anterior region of the pharynx*, 9 (fig. 24), the *muscle of hypopharyngeal bar Y*, 10 (fig. 23), and the *compressor muscle group of the cibarium*, 12 (fig. 24), are all similar to those in *Harpalus*. The *dorsal dilator muscle of the pharynx*, 11, is absent. Bar *Y* is also continuous with a subpharyngeal support. There is an apodeme originating in the anterior gular region essentially the same as the one in *Harpalus*; however, only the *dorsal and ventral muscles of the labium*, 20 and 21 respectively (fig. 23), arise on it. The *muscle of the hypopharynx*, 19 (figs. 23, 25), arises by means of a T-shaped tendon, the lateral arms of which originate on the walls of the gular suture. The musculature of *D. vittatus* is practically the same as that in *D. discolor*.

The larvae used for study are *Dineutes* sp. (figs. 26, 27, 28). The *dorsal dilator muscles of the cibarium*, 5, 6, and 7, and the *muscle of hypopharyngeal bar Y*, 10 (figs. 26, 28), are similar to those of the larva of *Amara* sp.; they are proportionately much more massive. The *dorsal dilator muscle of the pharynx*, 11, is present and the *compressor muscle group of the cibarium*, 12, is either absent or so poorly developed that it is not noticeable. The labial muscles are essentially the same as those of *Amara* with some variation as to shape. The *muscle of the prementum*, 22 (figs. 27, 28), is present in *Dineutes*.

## V. STAPHYLINOIDEA

The adults studied in this superfamily are *Silpha americana* L., Silphidae (figs. 29, 30, 31), and *Crcophilus villosus* Grav., Staphylinidae. In *Silpha* the labral muscles are present. The *compressor muscle of the labrum*, 1, is well developed (fig. 31), and the *ventral muscle of the labrum*, 3 (fig. 31), is inserted on the labrum by means of a long, thin tendon. The *dorsal dilator muscles of the cibarium*, 5, 6, and 7 (figs. 29, 31), the *compressor muscle group of the cibarium*, 12 (figs. 29, 31), the *dorsal dilator muscles of the pharynx*, 9 and 11 (figs. 29, 31), and the *muscle of hypopharyngeal bar Y*, 10 (figs. 29, 31), are all massive and undoubtedly furnish the power for a strong and efficient sucking mechanism. The musculature of the labium is essentially the same as that found in *Periplaneta*, excepting the salivary muscles, which are not found in Coleoptera. The *muscle of the hypopharynx*, 19 (figs. 30, 31), the *dorsal and ventral muscles of the labium*, 20 and 21 (figs. 30, 31), the *muscle of the prementum*, 22 (figs. 30, 31), and the *levator muscle of the labial palpus*, 24 (fig. 30), are present. The preoral cavity is provided with a sizeable, narrow lobe (fig. 31) that extends downward from the cibarial wall and also is equipped with a suboral grooved shelf (fig. 31) that originates in the posterior dorsal region of the labium, and which receives the cibarial lobe in somewhat of a semi-piston-and-cylinder relationship, possibly to facilitate sucking operations.

In *Crcophilus* the labial muscles are the same in number and arrangement as in *Silpha*; they arise slightly more posteriorly on the gular sutures. The labral muscles are similar also except that the *ventral muscle of the labrum*, 3, arises on the anterior surface of the distal end of the anterior tentorial arm at the junction of the arm and the head wall. The muscles of the cibarial and pharyngeal regions are practically the same as those found in *Silpha*.

*Silpha americana* L., Silphidae (figs. 32, 33, 34), and a specimen of Staphylinae of the Staphylinidae are the two larval forms used for study. The muscles in *Silpha* are very well developed. The *compressor muscle of the labrum*, 1, is absent and the *ventral muscle of the labrum*, 3 (figs. 32, 34), is strong. The *dorsal dilator muscles of the cibarium*, 5, 6, and 7 (figs. 32, 34), have become grouped together in a large mass. The *compressor muscle group of the cibarium*, 12 (figs. 32, 34), is well developed as are the *dorsal dilator muscles of the pharynx*, 9 and 11 (figs. 32, 34). The *muscle of hypopharyngeal bar Y*, 10 (fig. 34), is strong and multibranched. Muscle 11A (fig. 34), is an additional dorsal dilator of the pharynx which possibly belongs to the *dorsal dilator muscle group of the pharynx*,



11. The labium is a good example of the prementum with two divisions 1 and 2 (fig. 33). The *muscle of the hypopharynx*, 19 (figs. 33, 34), the *dorsal and ventral muscles of the labium*, 20 and 21 (figs. 33, 34), and the *muscle of the prementum*, 22 (fig. 34), are all present, well developed, and take their origin on the tentorial structure. In the specimen of Staphylinae the *muscle of the prementum*, 22, is inserted on the prementum at the base in the same plane as the *dorsal and ventral muscles of the labium*, 20 and 21. The prementum is not divided into two parts as in *Silpha*. The cibarial, pharyngeal, and hypopharyngeal muscles are much the same as those in *Silpha*, with a few variations. The labral muscles are absent; a tendon arises on the anterior tentorial arm, dorsal region, and extends anteriorly to be inserted basally and laterally on the nasale in a manner very similar to the insertion of the *ventral muscle of the labrum*, 3, in the adult *Creophilus villosus* Grav.

## VI. HYDROPHILOIDEA

*Sphaeridium scaraboides* Linn., Hydrophilidae (figs. 35, 36, 37), is the adult form studied. The muscles, though well developed, are reduced in number. Muscle 1 (fig. 35) possibly corresponds with the *compressor muscle of the labium*, 1, in *Periplaneta*; the insertion has become changed from the ventral wall of the labrum to a sclerotized mesal extension of the torma which is continuous with the dorsal wall of the anterior region of the cibarium. The *ventral muscle of the labrum*, 3 (figs. 35, 37), arises on the distal end of the dorsal branch of the anterior tentorial arm and is inserted in the usual way. The *dorsal dilator muscles of the cibarium*, 5, 6, and 7, are absent. The anterior tentorial arms are joined by a sclerotized suboesophageal brace, SB (fig. 37); a lateral dilator muscle of the pharynx arises on this brace. The *dorsal and ventral muscles of the labium*, 20 and 21 (figs. 36, 37), both take their origin in the anterior area of the postmental region.

*Sphaeridium bipustulatum* Fabr. (figs. 38, 39, 40) and *Hydrous triangularis* (Say) are the larvae studied in the family Hydrophilidae. In *Sphaeridium* the labral muscles are absent. The *dorsal dilator muscles of the cibarium*, 6 and 7 (figs. 38, 39), are present; muscle 6 is long, 7 compact and linear. The *dorsal dilator muscles*, 9 and 11 (fig. 39), are well developed as is also the *muscle of hypopharyngeal bar Y*, 10 (fig. 39). Bar Y is continuous with the sclerotized subpharyngeal area. The three muscles 36, 37, and 38 (fig. 39) are probably maxillary muscles. Muscle 36 arises laterally from the posterior region of this sclerotized subpharyngeal area and 37 and 38



arise on a median apodeme in the posterior gular region; all these muscles are inserted at the base of the maxilla. There is a small labial muscle, probably the *ventral muscle of the labium*, 21 (figs. 39, 40), that arises at the base of the postmentum adjacent to the posterior tentorial pits; it is inserted medially and basally on the prementum.

In *Hydrous* there are five pairs of powerful muscles that arise on the anterior tentorial arm and are inserted at the base of the maxilla. There is a muscle present, probably the *ventral muscle of the labium*, 21, and another that is inserted on the dorsal region of the labium which may be the *dorsal muscle of the labium*, 20. The *dorsal dilator muscles of the cibarium*, 6 and 7, the *dorsal dilator muscles of the pharynx*, 9 and 11, the *muscle of hypopharyngeal bar Y*, 10, and the *compressor muscle group of the cibarium* are all similar to those in *Sphaeridium* though they are much more massive. The ventral muscles of the pharynx are large and complicated in arrangement.

#### VII. CUCUJOIDEA

In this group *Scotobates calcaratus* (Fab.), Tenebrionidae, and *Epilachna corrupta* Muls., *Hippodamia convergens* Guer., Coccinellidae, adults were used for study. In *Scotobates* (figs. 41, 42, 43) the labral, cibarial, pharyngeal, and hypopharyngeal muscles are present and well developed. Bar *Y* (fig. 41) is connected with the anterior, distal edge of the anterior tentorial arm by means of a flat, sclerotized band. The *ventral muscle of the labium*, 21 (figs. 41, 42), may be homologous with that of *Periplaneta*, but its origin is on the anterior region of the postmentum and not on the tentorium. The *dorsal muscle of the labium*, 20 (figs. 41, 42), arises in the usual manner, but it is inserted medially on the inner side of the anterior labial wall and might easily be interpreted as the *muscle of the hypopharynx*, 19.

In *Epilachna* there is only one labial muscle; it corresponds with the *ventral muscle of the labium*, 21, in *Scotobates*. The muscles of the labrum, cibarium, and pharynx are essentially the same as those in *Scotobates*, with a slight variation in arrangement. The *muscle of hypopharyngeal bar Y*, 10, lies laterad of the *ventral muscle of the labrum*, 3. The *dorsal dilator muscles of the pharynx* are very powerful.

In *Hippodamia convergens* Guer. the musculature is practically the same as in *Epilachna*. The *compressor muscle group of the cibarium*, 12, is well developed.

*Scotobates calcaratus* (Fab.), Tenebrionidae, *Hippodamia convergens* Guer., Coccinellidae, and *Synchroa puncta* Newm., Syn-

chroidae, larvae were studied. In *Scotobates* (figs. 44, 45, 46) the muscles are well developed. The *compressor muscle of the labrum*, 1, the *dorsal dilator muscle of the pharynx*, 11, and the *compressor muscle group of the cibarium*, 12, are absent. The *dorsal dilator muscles of the cibarium*, 5, 6, and 7 (figs. 44, 46), have become grouped together and are indicated only by 7. The *muscle of hypopharyngeal bar Y*, 10 (fig. 44), has numerous subdivisions. There is a large, heavily sclerotized median cuspidate sclerite (CPS) on the dorsal surface of the hypopharynx (fig. 46). An arm extends posteriorly and ventrally from each side of the posterior region of this sclerite to become joined to a heavily sclerotized intralabial brace the lateral limits of which are the sides of the posterior hypopharyngeal region. The *ventral muscle of the labium*, 21 (figs. 45, 46), arises and is inserted in the usual manner; the *dorsal muscle of the labium*, 20 (fig. 46), arises in the posterior lateral region of the submentum just anterior to the posterior end of the anterior tentorial arm. The *muscle of the prementum*, 22 (fig. 45), is a broad, powerful muscle.

In *Hippodamia* only the *ventral muscle of the labium*, 21, is present. The *ventral muscle of the labrum*, 3, is absent; the tormae are slender and rodlike and extend posteriorly to become united with hypopharyngeal bar Y. The *dorsal dilator muscles of the pharynx*, 9 and 11, are especially powerful.

In *Synchroa* the musculature is similar to that of *Scotobates* though the *compressor muscle group of the cibarium*, 12, is present and the *muscle of hypopharyngeal bar Y*, 10, is not so profusely branched.

#### VIII. BYRRHOIDEA

Only larval forms were available for study in the family Byrrhidae. In *Byrrhus* (figs. 47, 48, 49) the labral muscles are absent. The *dorsal dilator muscles of the cibarium*, 5, 6, and 7 (figs. 47, 48), are reduced in size and are grouped together. The *dorsal dilator muscle of the anterior region of the pharynx*, 9 (figs. 47, 48), is small; the *muscle of hypopharyngeal bar Y*, 10 (figs. 47, 48), consists of two large branches, 10 and 10A. The labial muscles are somewhat confusing because of an additional labial muscle, 22A (figs. 48, 49). The regular labial muscles, 20 and 21, occur as usual and the *muscle of the prementum*, 22 (figs. 48, 49), is consistent. The additional labial muscle, 22A, may be a second muscle of the prementum inserted at the base of prementum 1 (figs. 48, 49).

## IX. DASCILLOIDEA

From this superfamily adult and immature stages of *Nosodendron californicum* Horn, Nosodendridae, and *Heterocerus* sp., Heteroceridae, larvae were studied. In the adult *Nosodendron* (figs. 50, 51, 52), of the labral muscles only the *ventral muscle of the labrum*, 3 (figs. 51, 52), is present. The cibarial, pharyngeal, and hypopharyngeal muscles are well developed. The *muscle of hypopharyngeal bar Y*, 10 (figs. 51, 52), is especially massive. Bar Y (fig. 52) is greatly modified; it forms a strong, lateral support to the mouth and is continuous with a broad, thin, sclerotized structure that extends ventrally and posteriorly to become united with the ventral head wall. The *dorsal and ventral muscles of the labium*, 20 and 21 (figs. 50, 52), are present; they originate in the gular area posterior to the submentum. The mentum completely covers the prementum in this species (fig. 52).

In the larval *Nosodendron* (figs. 53, 54, 55) the labral muscles are absent as is also the *compressor muscle group of the cibarium*, 12 (fig. 54). The *dorsal dilator muscles of the cibarium*, 5, 6, and 7, the *muscle of hypopharyngeal bar Y*, 10, and the *dorsal dilator muscles of the pharynx*, 9 and 11, are all massive and are collected more or less in the region of the posterior area of the cibarium (figs. 53, 54). Bar Y (fig. 54) is large and forms a strong support on the sides of the mouth; it extends ventrally on the sides of the posterior hypopharyngeal region. The full complement of labial muscles is present.

In *Heterocerus* the labral, cibarial, pharyngeal, and hypopharyngeal muscles are similar to those of *Nosodendron*; the *muscle of hypopharyngeal bar Y* is trifurcate. The *dorsal muscle of the labium*, 20, arises at the posterior end of the anterior tentorial arms and is inserted on the dorsal wall of the labium at what is probably the base of the hypopharynx. The *ventral muscle of the labium*, 21, takes its origin medially in the posterior region of the postmentum and is inserted medially at the base of prementum 1. Muscle 22 (probably the *muscle of the prementum*) originates on a transverse bar that connects the anterior tentorial arms; it is inserted laterally in the posterior region of prementum 2.

## X. DRYOPOIDEA

*Helichus fastigiatus* (Say), Dryopidae (figs. 56, 57, 58), is the adult form selected for study from this superfamily. The musculature in this species is, with some modification, of the generalized plan. The *compressor muscle group of the cibarium*, 12, is absent

as also is the *anterior dorsal dilator muscle of the pharynx*, 9, and the *dorsal dilator muscle of the cibarium*, 5. Hypopharyngeal bar *Y* (fig. 57) is very weakly sclerotized. The labial muscles consist of two pairs, the *dorsal and ventral muscles of the labium*, 20 and 21 (figs. 57, 58).

The larvae considered from the family Ptilodactylidae are *Ptilodactyla serricollis* (Say) (figs. 59, 60, 61). The *ventral muscle of the labrum*, 3, two *dorsal dilator muscles of the cibarium*, 6 and 7, and the *muscle of hypopharyngeal bar Y*, 10 (figs. 59, 61), are present and well developed. The *dorsal and ventral muscles of the labium*, 20 and 21 (figs. 60, 61), are present. Muscle 20 originates medially at the inner base of the anterior tentorial arms; muscle 21 arises on the base of the submentum between the posterior ends of the anterior tentorial arms.

#### XI. CANTHAROIDEA

Adults from two families in this group were studied, *Chauliognathus pennsylvanicus* Deg., Cantharidae, and *Plateros timidus* Lec., Lycidae.

In *Chauliognathus* (figs. 62, 63, 64) the muscles are very well developed; those of the labrum, cibarium, pharynx, and hypopharynx are massive (figs. 62, 63). The transverse *compressor muscle group of the cibarium*, 12, is absent. Hypopharyngeal bar *Y* (fig. 62) is continuous with the greatly modified tentorial structure that forms a strong support to withstand the action of the powerful muscles of this region; it unites the dorsal and ventral head walls rigidly. One side of the structure is joined with the other by means of a subpharyngeal sclerotized area. The posterior (ventral) ends are continuous with the ventral head wall. The epipharyngeal region of the labrum and the posterior dorsal labial region are equipped with a lobe and a grooved receptacle respectively, similar to that already described in the adult *Silpha americana* L., but in *Chauliognathus* it is more definitely associated with the epipharyngeal area. The labial muscles are much the same as those of the generalized form and are not nearly so powerful proportionately as are those of the dorsal head regions. Each lateral posterior margin of the labium is furnished with a slender, sclerotized resilient bar, *RB* (fig. 62), which abuts against the anterior external face of the rigid tentorial structure. This resilient bar probably assists the labium in returning to its normal resting position after contractions of the labial muscles have disturbed its position.



In *Plateros* there is only one pair of labial muscles, the ventral pair, 21; they arise on the posterior ends of the anterior tentorial arms and are inserted medially on the base of the prementum. The *levator muscle of the labial palpus*, 24, is present. The rigid tentorial structure that was found in *Chauliognathus* is absent in *Plateros*. The labral, cibarial, pharyngeal and hypopharyngeal muscles are all essentially the same as in *Chauliognathus*.

*Chauliognathus pennsylvanicus* Deg., Cantharidae (figs. 65, 66, 67), and *Photuris* sp., Lampyridae, are the larval forms considered.

In *Chauliognathus* (figs. 65, 66) muscle 5 does the same work as the *dorsal dilator muscle of the cibarium*, 5 (figs. 1, 2), in the generalized form; it is considered homologous though it is greatly modified in origin and somewhat in its insertion. The other *dorsal dilator muscles of the cibarium*, 6 and 7 (figs. 65, 67), form a compact, linear group as do also the *dorsal dilator muscles of the pharynx*, 11 (fig. 67). There is a heavy tentorial modification present, but it is less extensive than that of the adult; it is also continuous with the subpharyngeal plate. Hypopharyngeal bar Y (fig. 67) extends posteriorly from the dorsal region of the structure. There is a heavily sclerotized postoral subpharyngeal support that joins the head on each side laterad of the mouth. The labial muscles are similar to those of the adult and the posterior lateral sclerotized resilient bar, RB (fig. 67), that was described in the adult form is also present in the larvae.

In *Photuris* sp. the musculature is similar to that of *Chauliognathus*; the muscles, however, are less well developed.

## XII. ELATEROIDEA

*Neotrichophorus carolinensis* (Schfr.), Elateridae, and *Chrysobothris femorata* (Oliver), Buprestidae, are the adult forms from this group used for study.

In *Neotrichophorus* (figs. 68, 69, 70) the full complement of labral muscles is present. Upon first examination it was thought that only the *ventral muscle of the labrum*, 3 (figs. 68, 70), was present, but it was later determined that muscle 3 and the *dorsal muscle of the labrum*, 4, are so closely appressed as to appear as one. Muscle 4 is inserted laterally on the posterior dorsal rim of the labrum while muscle 3 is inserted ventrally and laterally as is the usual manner. This is the only species in the order Coleoptera, examined in this work, that exhibited any indication of an anterior (dorsal) labral muscle. Another elaterid adult, *Heteroderes nicholsi* Notman, was



examined, but only the *ventral muscle of the labrum*, 3, was found to be present; muscle 3 in this species is unusual in that it originates laterally in the anterior clypeal region (fig. 74). This condition has been observed only in this species.

In *Neotrichophorus* the cibarial, pharyngeal, and hypopharyngeal muscles are of the usual form (figs. 68, 70). Hypopharyngeal bar *Y* more or less parallels the lateral margins of the cibarium and is joined to the bar *Y* on the opposite side by a subpharyngeal supporting area on which are inserted strong *ventral dilator muscles of the pharynx*, 30 (fig. 68). The labial and hypopharyngeal muscles are of generalized form, though the *ventral muscle of the labium*, 21, is absent unless the *muscle of the prementum*, 22 (figs. 68, 69), has been misinterpreted as 21, in which case, of course, muscle 22 would be absent.

In *Chrysobothris* the labial and palpal muscles are similar to those in *Neotrichophorus*; the *muscle of the prementum*, 22, is absent. The labral muscles are also similar except that the *dorsal muscle of the labrum*, 4, is absent; the *ventral muscle of the labrum*, 3, arises in the midfrontal region on the inner (mesal) surface of the suture that separates the inner margin of the compound eye from the frons. The cibarial, pharyngeal, and hypopharyngeal muscles are essentially the same, but are all poorly developed.

*Parallelostethus attenuatus* (Say) (figs. 71, 72, 73), *Alaus* sp., Elateridae, and *Cebrio antennatus* Schfr., Cebriionidae, are the larvae studied in this superfamily.

In *Parallelostethus* the labral muscles are absent. The cibarial, pharyngeal, and hypopharyngeal muscles are powerful, but otherwise similar to those found in the adult *Neotrichophorus*; hypopharyngeal bar *Y* is also similar. The labial muscles, except for being long and thin (figs. 72, 73), are of the generalized form. The extra length is made possible by a posterior, spurlike extension of the anterior tentorial arm (fig. 73); the *dorsal and ventral muscles of the labium*, 20 and 21, arise on the inner surface on the posterior tip of this spurlike extension.

In *Alaus* sp. the musculature is essentially the same as that in *Parallelostethus*, and in the cebriionid larva, *Cebrio*, the muscles were found to be practically the same as those in the two elaterid larvae studied.

### XIII. SCARABAEOIDEA

The adults of *Popillia japonica* Newman and *Macrodactylus subspinosus* (Fab.), Scarabaeidae, and *Lucanus placidus* Say, Lucanidae, were selected for study in this superfamily.

In *Popillia* (figs. 75, 76, 77), of the labral muscles only the *ventral muscle of the labrum*, 3 (figs. 75, 76), is present. The cibarial, pharyngeal, and hypopharyngeal muscles are similar to those of the generalized plan except that the *dorsal dilator muscle of the pharynx*, 11, is absent. *Muscle group 13* (figs. 75, 76) may or may not be homologous with the *compressor muscles of the anterior region of the cibarium*, 13 (fig. 2), in *Periplaneta*; they are well-developed diagonal muscles inserted on the anterior dorsal wall of the cibarium and they apparently have the same function. The *compressor muscle group of the cibarium*, 12 (fig. 75), is wide, but not long and it is confined to the posterior dorsal region of the cibarium. There is only one labial muscle present, 39 (figs. 76, 77); it is a single unit of fibers arising centrally in the middle region of the labium and extending slightly anteriorly and dorsally to become inserted medially on the dorsal labial wall. The function, probably, is to assist in moving the hypopharyngeal region in some manner. The *levator muscle of the labial palpus*, 24 (fig. 77), arises on an intralabral tormalike process extending mesad from the lateroventral base of the labium; this structure extends in a hoop form dorsally and is joined to the process on the opposite side of the labium. The tendinous insertion end of one of the maxillary muscles enters the intralabial region (fig. 77) and extends through the modified, hoop-like structure to be inserted on the maxillary base; it has no effect on the movement of the labium.

In *Macroductylus* the *median labial muscle*, 39, is absent; a muscle probably corresponding to the *ventral muscle of the labium*, 21, of the generalized form arises rather medially in the anterior region of the postmentum and is inserted ventrally on the base of the prementum. The cibarial, pharyngeal, and hypopharyngeal muscles are similar to those in *Popillia*; the *compressor muscles of the anterior region of the cibarium*, 13, are absent as is also the *ventral muscle of the labrum*, 3.

In *Lucanus* the *median labial muscle*, 39, and the *ventral muscle of the labrum*, 3, are absent; the *ventral muscle of the labium*, 21, is similar to that in *Macroductylus*. The *muscle of hypopharyngeal bar Y*, 10, is large and branched because of the fact that bar Y has a wide, thin, multibranched distal end, and muscle 10 is, of course, inserted on these distal branches. There is a muscle group present that possibly is homologous with the *compressor muscles of the anterior region of the cibarium*, 13, in *Popillia*; the fibers are arranged on the dorsal wall of the cibarium more longitudinally than diagonally, which is the case in *Popillia*. The cibarial muscles are all

rather slender and the oesophagus is small considering the size of the insect.

The larval forms of Scarabaeoidea studied pertain to *Popillia japonica* Newman and *Cotinis nitida* (L.), Scarabaeidae.

In *Popillia* (figs. 78, 79, 80) the *ventral muscle of the labrum*, 3 (figs. 78, 79), is strong; the *muscle of hypopharyngeal bar Y*, 10 (figs. 78, 79), is massive. All of the cibarial muscles are absent. The *dorsal dilator muscle of the anterior region of the pharynx*, 9 (fig. 78), is so weak as to be almost threadlike. The *compressor muscle group of the cibarium*, 12 (fig. 78), is poorly developed. There is a large, heavily sclerotized cuspidate sclerite on the posterior dorsal surface of the labium. The *dorsal and ventral muscles of the labium*, 20 and 21 (figs. 78, 80), and the *muscle of the prementum*, 22 (figs. 78, 80), are well developed.

In *Cotinis* the labral and labial muscles are similar to those in *Popillia*; the *muscle of hypopharyngeal bar Y*, 10, is also similar. There is only one pair of weak muscles inserted on the dorsum of the cibarium just anterior to the frontal connective nerves; it is probably one of the *dorsal dilator muscles of the cibarium*, 5, 6, or 7. A pair of weak dorsal pharyngeal muscles, probably 9, is present.

#### XIV. CLEROIDEA

*Dermestes caninus* Germ., Dermestidae, and *Enoclerus spinolae* Lec., Cleridae, are the adult forms studied in this superfamily.

In *Dermestes* (figs. 81, 82, 83) the labral, cibarial, pharyngeal, and hypopharyngeal muscles are all well developed. The *compressor muscle of the labrum*, 1, and 5 of the *dorsal dilator muscles of the cibarium* are absent. The *muscle of hypopharyngeal bar Y*, 10 (figs. 81, 82), is branched as in the generalized form. Bar *Y* is rather heavy and is continuous ventrally with a sclerotized subpharyngeal rod that connects the bar *Y* of one side with that of the other. In the labium a muscle is present that might be considered either as the *muscle of the prementum*, 22, or as the *ventral muscle of the labium*, 21 (figs. 81, 83). It arises medially in the anterior region of the submentum and is inserted medially on the base of the prementum. The muscle 20 (figs. 81, 83) may in reality be homologous with the *muscle of the hypopharynx*, 19; it arises on the inner surface of the posterior end of the anterior tentorial arm and is inserted medially on the dorsal labial wall in the anterior region by means of a tendon.

In *Enoclerus* the musculature is similar to that in *Dermestes*, with a few variations. One additional pair of ventral muscles of the labium is present.

For the larval stages, *Dermestes caninus* Germ., Dermestidae, and *Tenebriodes* sp., Ostomatidae, were chosen for study.

In *Dermestes* (figs. 84, 85, 86) the labral muscles are absent; the dorsal dilator muscle of the cibarium, 5, the dorsal dilator muscle of the pharynx, 11, and the compressor muscle group of the cibarium, 12, are also absent. The other cibarial, pharyngeal, and hypopharyngeal muscles are present and well developed. The muscle of hypopharyngeal bar *Y*, 10 (figs. 84, 85), is branched and especially massive. Bar *Y* (fig. 84) is heavily sclerotized and forms a rigid lateral support to the dorsal cibarial region and to the mouth. As is the case in the adult *Dermestes*, the labial muscle, 21 (figs. 84, 86), is difficult to homologize with those of the generalized form; the selection of their numerical designations (names), in this case, is influenced entirely by their points of insertion.

In *Tenebriodes* sp. the ventral muscle of the labrum, 3, is present. The cibarial, pharyngeal, hypopharyngeal, and labial muscles are similar to those of *Dermestes*; the ventral muscle of the labium, 21, arises on the tentorial structure and not on the submentum as it does in *Dermestes*.

#### XV. MELOIDEA

*Macrobasis immaculata* (Say), Meloidae (figs. 87, 88, 89), is the adult studied in this superfamily. The labral muscles, 1 and 3 (figs. 87, 88), are present and well developed. The dorsal dilator of the cibarium, 5, is absent; the compressor muscle group of the cibarium, 12, is weak; the other cibarial and pharyngeal muscles are strong. The proximal (ventral) region of bar *Y* (fig. 88) supports the ventral pharyngeal wall and the sides of the mouth. In the labium the levator muscle of the labial palpus, 24 (figs. 88, 89), takes its origin on the intralabial sclerotized bar, *IR* (fig. 88), that terminates laterally in a broad lateral hypopharyngeal sclerite. The muscle of the hypopharynx, 19 (figs. 88, 89), arises in the usual area and is inserted medially on a short apodeme process by means of a tendon.

The larva studied is *Zonabris phalerata* (Pall.) (figs. 90, 91, 92). The muscles are well developed in this species, though the compressor muscle of the labrum, 1, and the dorsal dilator muscle of the cibarium, 5, are absent. The dorsal muscle of the labium, 20 (figs. 91, 92), arises in the posterior region of the submentum and the ventral muscle of the labium, 21 (figs. 91, 92), originates medially in the anterior region. Hypopharyngeal bar *Y* (fig. 91) is continuous with a long sclerotized subpharyngeal structure that joins the two bars together in the posterior region of the ventral wall of the cibarium.



## XVI. MORDELLOIDEA

*Mordella quadripunctata* (Say), Mordellidae (figs. 93, 94, 95), is the adult form used for study in this superfamily. The muscles are powerful and well developed. The cibarial, pharyngeal, and hypopharyngeal muscles are of the generalized form. Hypopharyngeal bar *Y* (fig. 93) is weakly sclerotized. The *muscle of the prementum*, 22 (fig. 95), might be the *ventral muscle of the labium*, 21, with the origin moved anteriorly from the tentorial structure rather than muscle 22, though it is difficult to interpret a condition like this. The *ventral dilator muscle of the pharynx*, 30 (fig. 93), and the *lateral dilator muscle of the pharynx*, 31 (fig. 93), are present, the latter being very large. There is a sclerotized subpharyngeal rod (fig. 93) that lies immediately under the mouth opening; it terminates laterally in the integument of the posterior dorsal hypopharyngeal area.

The larvae studied are of the same species as the adult (figs. 96, 97, 98). The musculature is, as the figures indicate, well developed and unusual. There is a large, thin, sclerotized apodeme that extends ventrally from the center of the middle region of the frons on which the *ventral muscle of the labrum*, 3 (fig. 97), the *muscle of hypopharyngeal bar Y*, 10, 10A, 10B (fig. 97), and the *dorsal dilator muscle of the pharynx*, 11 (fig. 97), all take their origin. The *ventral muscle of the labrum*, 3 (figs. 96, 97), is inserted on the distal end of a modified tormia that originates on the ventral labral wall and which extends laterally and dorsally. The *dorsal dilator muscles of the cibarium*, 6 and 7 (fig. 97), are thin and very long; the *muscle of hypopharyngeal bar Y*, 10, 10A, 10B (fig. 97), is divided into three branches and the *dorsal dilator muscle of the pharynx*, 11 (fig. 97), originates on the ventral margin of the posterior region of the apodeme. The labial muscles, 20 and 22 (figs. 97, 98), do not require special comment as the figures are self-explanatory. There is present a rigid, heavily sclerotized, subpharyngeal intralabial structure, 1R (fig. 97). The crosspiece that lies beneath the anterior region of the pharynx terminates in the lateral integumental wall of the posterior labial or hypopharyngeal region.

## XVII. CERAMBYCOIDEA

The adults studied in this superfamily are *Cyllene robiniae* (Forst.), Cerambycidae, Cerambycinae, and *Prionus pocularis* Dalm., Prioninae.

In *Cyllene* (figs. 99, 100, 101) the muscles are well developed and are of the generalized plan. The *muscle of hypopharyngeal bar Y*,



10 (figs. 99, 100), is especially massive. The dorsal wall of the cibarium is decidedly dome-shaped and appears to be able to accommodate the suboral lobe, *SL* (fig. 99). The *dorsal muscle of the labium*, 20 (figs. 99, 101), is inserted laterally on the prementum near the dorsal surface. In the posterior lateral region of the subpharyngeal area the integument of one side is joined with that of the opposite by a sclerotized intralabial rod, *IR* (fig. 99). The anterior tentorial arm (fig. 99, *AT*) is broad but thin. The suboral lobe (*SL*) is probably the hypopharynx; a muscle interpreted as the *muscle of the hypopharynx*, 19 (figs. 99, 101), is inserted medially at its base.

In *Prionus* the *compressor muscle of the labrum*, 1, is absent; the *muscle of hypopharyngeal bar Y*, 10, is branched. The labral, cibarial, pharyngeal, and hypopharyngeal muscles are similar to those in *Cyllene*. The labial muscles are similar also, except that the *muscle of the prementum*, 22, is absent and the *ventral muscle of the labium*, 21, is present.

In the larval *Cyllene robiniae* (Forst.), Cerambycinae (figs. 102, 103, 104), the muscles are powerful and in the dorsal head region are usually multibranched or subdivided. The labral muscles are absent; the *dorsal dilator muscles of the cibarium*, 5, 6, and 7 (figs. 102, 104), occur in groups and the *muscle of hypopharyngeal bar Y*, 10 and 10A (fig. 104), consists of two main branches each of which is subdivided into several units. The *compressor muscle group of the cibarium*, 12 (figs. 102, 104), is strong; immediately beneath this group the dorsal wall of the posterior region of the cibarium and the anterior pharyngeal region invaginates to form a pouch which, when viewed laterally, is somewhat obovate. This pouch or lobe extends down into the region of the mouth opening. There is a median muscle, 40, beneath the *compressor muscle group of the cibarium*, 12 (figs. 102, 104), that arises medially in the posterior region of the pouch and is inserted centrally in the anterior region of the same. The *dorsal dilator muscle of the pharynx*, 11 (fig. 104), is inserted on the posterior dorsal region of the pouch and the *dorsal dilator muscle of the cibarium*, 7, in the anterior dorsal region. By the combined action of muscles 7, 11, 12, and 40 (fig. 104) it would seem that the lobe formed by the ventral wall of the pouch could pull food into the mouth from the shelflike hypopharynx, *HY*, that lies immediately anterior to it. In the ventral head region the *muscle of the hypopharynx*, 19, the *dorsal and ventral labial muscles*, 20 and 21, the *ventral and lateral dilator muscles of the pharynx*, 30 and 31

(figs. 103, 104), are all well developed and conform rather closely to the generalized plan of musculature.

#### XVIII. BOSTRICHODEA

*Apatides fortis* (Lec.), Bostrichidae, adult and immature forms, were used for study in this superfamily.

In the adult *Apatides* (figs. 105, 106, 107) the epipharynx is large and conelike; the *compressor muscle of the labrum*, 1 (fig. 106), is elongate and is inserted laterally near the tip of the epipharynx. The epipharynx (fig. 106, *EP*) is supported laterally by a slender sclerotized rod (*SR*) arising dorsally on a tormalike process that extends mesad from the side of the labrum anterior to the base of the normal torma. The *ventral muscle of the labrum*, 3 (figs. 105, 106), is inserted on the distal end of the torma which is more elongate than usual. The cibarial, pharyngeal, and hypopharyngeal muscles are strong. The *dorsal dilator muscle of the cibarium*, 7 (figs. 105, 106), apparently has a branch, 7*A* (fig. 105), the point of origin of which has migrated anteriorly to the posterior surface of the epistomal suture. The labial muscles are well developed; the *ventral muscle of the labium*, 21 (figs. 106, 107), possibly in reality is the *muscle of the prementum*, 22, since it takes its origin laterally in the posterior region of the submentum.

The larval *Apatides* (figs. 108, 109, 110) exhibits the first *labral compressor muscle*, 1 (figs. 108, 109), observed in immature Coleoptera. The powerful *ventral muscle of the labrum*, 3 (figs. 108, 109), is inserted on the distal end of an elongate torma; the *muscle of hypopharyngeal bar Y*, 10 and 10*A* (fig. 108), is branched and strong. The *ventral and lateral dilator muscles of the pharynx*, 30 and 31 (fig. 108), are especially well developed. In the labium the *dorsal and ventral labial muscles*, 20 and 21 (figs. 108, 110), lie so close together that superficially they appear to be one muscle. The unusual muscle 41 (figs. 108, 110) was observed only in this species; it arises laterally in the anterior region of the submentum and extends dorsally almost vertically to become inserted laterally at the base of the labium near the dorsal surface.

#### XIX. CHRYSOMELOIDEA

*Leptinotarsa decimlineata* (Say), Chrysomelidae, *Donacia distincta* Lec., Donaciidae, and *Galerucella xanthomelaena* (Schr.), Galerucidae, are the specimens of adults studied in this superfamily.

In *Leptinotarsa* (figs. 111, 112, 113) the muscles of the dorsal head region are well developed. The *muscle of hypopharyngeal bar Y*,

10 (figs. 111, 112), is branched; the anterior branch 10A arises laterally in the anterior frontal area on the posterior surface of the epistomal suture. The labial muscles are strong, especially the *dorsal muscle of the labium*, 20 (figs. 112, 113). There is an unusual tendinous structure (fig. 112, TS) that arises broadly, medially and basally from the ventral labial wall; it extends anteriorly to be inserted medially on the dorsal wall of the labium in the anterior region. A contraction of the *dorsal labial muscle*, 20 (fig. 112), would exert a pull on the labium at the point of insertion; this tendon that joins the anterior dorsal labial surface with that of the posterior ventral region probably retracts the anterior labial area when muscle 20 contracts. There is a strongly sclerotized intralabial brace, IR (fig. 112), in the posterior region of the labium that terminates laterally in the integument.

<sup>1</sup> In *Donacia* the *compressor muscle of the labrum*, 1, is absent; the anterior branch of the *muscle of hypopharyngeal bar Y*, 10A, arises as it does in *Leptinotarsa*. The cibarial, pharyngeal, hypopharyngeal, labral, and labial muscles are apparently homologous with those found in *Leptinotarsa*.

In *Galerucella* the *compressor muscle of the labrum*, 1, is absent; the anterior branch of the *muscle of hypopharyngeal bar Y*, 10A, arises as it does in *Leptinotarsa*. The cibarial, pharyngeal, and labial muscles are homologous with those found in *Leptinotarsa*.

For the larvae in this superfamily *Leptinotarsa decimlineata* (Say) and *Typhophorus viridicyaneus* (Cr.), Chrysomelidae, were selected for study.

In *Leptinotarsa* (figs. 114, 115, 116) the muscles are very well developed. The *compressor muscle of the labrum*, 1 (figs. 114, 115), is present; the *cibarial muscles*, 6 and 7, and *pharyngeal muscles*, 11 (fig. 114), are long because of the space between the dorsal wall of the stomodaeum and the head wall. The *muscle of the hypopharyngeal bar Y*, 10 (fig. 114), is subdivided into many units. The *ventral dilator muscle of the pharynx*, 30 (fig. 114), is especially massive; the *dorsal and ventral labial muscles*, 20 and 21 (figs. 114, 116), and the *muscle of the prementum*, 22 (figs. 114, 116), are all strong. The latter muscle is inserted on the ventral wall of the labium on an area in which the division of the prementum is indistinct; the *dorsal and ventral labial muscles*, 20 and 21, are inserted on the base of prementum 1 (fig. 116). The *muscle of the prementum*, 22 (fig. 116), is inserted on the base of the second division of the prementum, though the dividing suture is indistinct.

The musculature in *Typhophorus* is similar to that of *Leptinotarsa* except that the *compressor muscle of the labrum*, 1, is absent.

## XX. PLATYSTOMOIDEA

*Euparius marmoreus* (Oliv.), Platystomidae (figs. 117, 118, 119), is the adult form studied in this superfamily. The labral muscles are absent; the cibarial, pharyngeal, and hypopharyngeal muscles are not well developed. The *hypopharyngeal bar Y* (fig. 118) is modified into a flat plate. There is a heavily sclerotized subpharyngeal rod, *IR* (fig. 118), present that supports the ventral region of the mouth and also strengthens the posterior lateral labial walls in which region the ends of the rod terminate. The labial muscles are well developed. The *dorsal muscle of the labium*, 20 (figs. 118, 119), is an unusual muscle in this species; it arises laterally in the posterior gular area as a thickened, powerful group of muscle fibers that quickly converge to become inserted on the end of a thin tendon in the anterior gular region. The tendon extends anteriorly and is inserted somewhat laterally in the dorsal region of the posterior labial area.

In the larva of this species (figs. 120, 121, 122) the *ventral muscle of the labrum*, 3 (figs. 120, 121), is present. The *muscle of hypopharyngeal bar Y*, 10 (fig. 10), is massive; the *dorsal dilator muscles of the pharynx*, 9 and 11, are absent in this species. The *hypopharyngeal bar Y* (fig. 121) is large; it supports the mouth opening laterally and is continuous with a heavily sclerotized suboral lobe that is joined on each side by a heavily sclerotized bar, *IR* (fig. 121), that terminates in the integumental wall of the posterior dorsal lateral region of the labium. The *ventral muscle of the labium*, 21 (figs. 121, 122), arises on the tentorium at the base of the tentorial arm; it is inserted medially on the base of the prementum. There is a division of the *muscle of the prementum*, 22 (figs. 121, 122), into two parts; each arises laterally in the anterior region of the submentum and each is inserted laterally at the base of the prementum.

## XXI. CURCULIONOIDEA

From this superfamily *Pantomorus godmani* (Crotch), Curculionidae, and *Dendroctonus valens* Lec., Scolytidae, were selected for study of the adults.

In *Pantomorus* (figs. 123, 124, 125) the muscles are reduced in number and those present are poorly developed. The *labial muscles* are absent and the *cibarial muscles*, 7 (figs. 123, 124), are represented by a row of weak fibers inserted through the transverse *compressor muscle group of the cibarium*, 12 (figs. 123, 124), and, since they all do insert through 12, are probably divisions of 7. The muscle of *hypopharyngeal bar Y*, 10 (fig. 123), is also weak and bar *Y* (fig.



123) has practically disappeared; it is very lightly sclerotized. There is a large, soft suboral lobe, *SL* (fig. 123), present that extends anteriorly into the cibarium in a tonguelike manner (fig. 123). The labium is furnished with a single pair of muscles (figs. 123, 125) that probably correspond with the *muscle of the prementum*, 22, in the generalized form.

In *Dendroctonus* the musculature is similar to that of *Pantomorus* with a few minor variations.

*Pantomorus leucoloma* Boh. and *Listroderes obliquus* Klug., Curculionidae, and *Eupsalis minuta* Drury, Brentidae, are the larval species studied.

In *Pantomorus* (figs. 126, 127, 128) the *ventral muscle of the labrum*, 3 (fig. 127), and the *muscle of hypopharyngeal bar Y*, 10 (fig. 127), are very well developed; the cibarial and pharyngeal muscles are rather weak. The *pharyngeal muscles*, 11 (fig. 127), are probably homologous with the *dorsal dilator muscles*, 11, in the generalized plan; they are inserted dorsally on the wall of the pharynx posterior to the frontal connective. *Hypopharyngeal bar Y* (fig. 127) is continuous with a broad lateral and ventral sclerotized plate that passes beneath the anterior region of the pharynx to become joined with the *bar Y* of the other side. A median, flat, sclerotized posterior extension arises from the posterior dorsal margin of the labrum (fig. 127, *ME*); it is a resilient piece. When the *ventral muscle of the labrum*, 3 (fig. 127), is retracted, the labrum is depressed and the sclerotized dorsal extension, *ME*, abuts against the posterior inner surface of the epistomal suture (fig. 127, *ES*). When the *ventral muscle of the labrum*, 3, relaxes, the resiliency of the extended process, *ME* (fig. 127), pushes the labrum back into its normal position thus doing the work of a muscle. There is a heavily sclerotized intra-labial rod, *IR* (fig. 127), present that terminates laterally on the posterior lateral walls of the labium and which is joined to the dorsal labial wall adjacent to the mouth opening. The labial muscles conform with those of the generalized form in origin and insertion.

In *Listroderes* the muscles are essentially the same as those in *Pantomorus*. The posterior dorsal margin of the labrum is furnished with the median posterior extension, *ME*, also. The *dorsal muscle of the labium*, 20, is inserted laterally on the dorsal wall of the labium.

The muscles in *Eupsalis* are similar to those of *Pantomorus*. The *dorsal muscle of the labium*, 20, is inserted as in the case of *Listroderes*. The *dorsal dilator muscle of the anterior region of the pharynx*, 9, is present in this species.



## XXII. LYMEXYLOIDEA

*Hylecoetus lugubris* Say, Lymexylidae, adults and larvae were selected for study in this superfamily.

The muscles of the labrum in the adult (figs. 129, 130) are represented only by the *ventral muscle of the labrum*, 3. The *pharyngeal muscles*, 9 and 11 (figs. 129, 130), occur in paired groups. The *muscle of hypopharyngeal bar Y*, 10 (fig. 129), lies between the two branches of *pharyngeal muscle*, 9. A small, longitudinal band of muscles, 13 (figs. 129, 130), is present; it possibly is homologous with the *compressor muscles of the anterior region of the cibarium*, 13 (fig. 2), of the general plan. They arise medially, adjacent to the anterior margin of *compressor muscle group of the cibarium*, 12 (figs. 129, 130), and are inserted medially and dorsally on the cibarium a short distance anterior to the point of origin. *Hypopharyngeal bar Y* (fig. 130) is rather large and furnishes a strong support to the sides of the mouth and to the posterior lateral cibarial region. The *lateral dilator muscle of the pharynx*, 31 (fig. 130), is long and powerful. The *muscle of the prementum*, 22 (figs. 130, 131), is the only muscle present in the labium.

In the larvae of *Hylecoetus* (figs. 132, 133, 134) the labral muscles are absent; the *muscle of hypopharyngeal bar Y*, 10, and its branch 10A (figs. 132, 133), are especially massive; the cibarial and pharyngeal muscles are comparatively long and slender. Muscle 10 (fig. 133) arises by means of a tendon in the posterior region of the frons. The posterior lateral labial region is furnished with a heavily sclerotized intralabial brace, *IR* (fig. 132), the ends of which terminate in the integumental wall. Externally there is a heavily sclerotized U-shaped area present that extends over the dorsal surface of the posterior labial region and is continuous laterally with the ends of the intralabial brace, *IR* (fig. 132). The labial muscles present an unusual plan of arrangement. The prementum is elongate and possesses a small median sclerite in the anterior region (fig. 134). The *muscle of the prementum*, 22 (figs. 132, 134), which is short and very broad, arises medially along the posterior margin of the tentorial bridge; it is inserted along the base of the prementum. The *ventral muscle of the labium*, 21 (figs. 132, 134), originates medially on the posterior margin of the tentorial bridge and it is inserted rather medially on the posterior edge of the median premental sclerite. The *dorsal muscle of the labium*, 20 (figs. 132, 134), arises laterally on the inner surface of the posterior end of the anterior tentorial arm; it is inserted laterally in the anterior region of the median sclerite of the prementum.

## SUMMARY

A general plan of muscle arrangement can be recognized in orthopteroid insects, and the same plan is found in representatives of other orders. It is possible to discover apparent homologies among muscles on the basis of origin and insertion, though one or both attachments may vary considerably among the different species. There are certain muscles that evidently are homologous with those of the generalized plan, but which because of some variation or modification in origin or insertion are difficult to identify. On the other hand, some muscles are aberrant and cannot be reconciled with any plan.

Some unusual muscles and structures, and relationships between muscles and skeletal parts, were encountered in this study.

The following muscles occurred only in the species of Orthoptera included in this work: the *hypopharyngeal muscle of the mandible*, 14 (fig. 1); the *anterior dorsal dilator muscle of the salivarium*, 15 (fig. 1); the *depressor muscle of the labial palpus*, 23 (fig. 1); the *muscles of the labial palpus*, 25, 26, and 27 (figs. 1, 3A); and the *flexor muscle of the glossa*, 28 (figs. 1, 3).

In *Periplaneta americana* L., Orthoptera, the *compressor muscle of the labrum*, 1 (fig. 2), is asymmetrical; the *dilator muscle group of the labrum*, 2 (fig. 2), and the *dorsal dilator muscle of the cibarium*, 8 (figs. 1, 1A, 2), were observed only in this species.

The *muscle of the hypopharynx*, 19 (figs. 5, 6), in *Anisolabis maritima* Gené, Dermaptera, arises centrally in the midregion of the mentum and not on the tentorial bridge as is the usual manner.

In both the adult and larval forms of *Corydalus cornutus* L., Neuroptera (figs. 9, 11), the prementum is divided into three sclerites. The muscle group 33 (fig. 11) was observed to be especially well developed only in the larva of *Corydalus*.

The two muscles 34 and 35 (figs. 14, 15) were observed only in the adult *Sphecius speciosus* (Dru.), Hymenoptera. The *muscle of hypopharyngeal bar Y*, 10, of the generalized plan is absent; this is the only case in which this condition was observed. The *dorsal muscle of the labium*, 20A (fig. 13), was found only in this species.

In *Harpalus caliginosus* F., Carabidae (adult), muscle 21A (fig. 19) is an additional labial muscle that is not found in the other insects included in this work. It is in this species also that the posttentorial apodeme, PTN (fig. 19), occurs; all of the labial muscles arise on this structure, as does also the *muscle of the hypopharynx*, 19 (fig. 19). A similar apodeme is found in *Dineutes discolor* Aube., Gyrinidae

(adult) (fig. 23, *PTN*), but the *hypopharyngeal muscle*, 19, does not originate on it in this species.

The prementum is divided into two sclerites in the coleopterous larvae of: *Silpha americana* L., Silphidae; *Byrrhus* sp., Byrrhidae; *Nosodendron californicum* Horn., Nosodendridae; *Hylecoetus lugubris* Say, Lymexylidae; and *Leptinotarsa decimlineata* (Say), Chrysomelidae. The *muscle of the prementum*, 22, occurs in all of these larvae; and the *muscle of prementum 1*, 22*A* (fig. 48), was found only in the larvae of *Byrrhus* sp., Byrrhidae.

In *Sphaeridium scarabaeoides* L., Hydrophilidae (adult), the *ventral muscle of the labrum*, 3 (figs. 35, 37), arises on the distal end of the anterior tentorial arm instead of on the dorsal head wall as is the usual manner. In *S. bipustulatum* Fabr. (larva) muscle 37 (fig. 39) arises on the posterior lateral margin of the subpharyngeal supporting area and is inserted on the base of the cardo; this muscle was not observed in other insects.

It was found that in *Scotobates calcaratus* (Fab.), Tenebrionidae (adult), the anterior tentorial arm, *AT* (fig. 41), is connected with *hypopharyngeal bar Y* by means of a thin, flat, sclerotized band.

A heavily sclerotized intralabial brace or rod (*IR*) that terminates laterally in the integument of the posterior lateral labial region is to be found in Coleoptera in: *Cyllene robiniae* (Forst.), Cerambycidae (adult) (fig. 99, *IR*); *Macrobasis immaculata* (Say), Meloidae (adult) (fig. 88, *IR*); *Leptinotarsa decimlineata* (Say), Chrysomelidae (adult) (fig. 112, *IR*); *Scotobates calcaratus* (Fabr.), Tenebrionidae (larva) (fig. 46, *IR*); *Mordella quadripunctata* (Say), Mordellidae (larva) (fig. 97, *IR*); *Pantomorus leucoloma* Boh., Curculionidae (larva) (fig. 127, *IR*); *Hylecoetus lugubris* Say, Lymexylidae (larva) (fig. 132, *IR*).

In *Nosodendron californicum* Horn., Nosodendridae (adults and larvae), the *hypopharyngeal bar Y* (figs. 52, 54) is greatly modified and enlarged (more so in the adult) and is continuous with the tentorial structure. In the adult form the mentum covers the prementum (figs. 50, 52).

In *Chauliognathus pennsylvanicus* Deg., Cantharidae (adults and larvae), the tentorial structure (figs. 62, 67, *TN*) is greatly modified (more so in the adult); a sclerotized resilient bar is present in the integument of the posterior lateral margin of the labium.

Only in *Neotrichophorus carolinensis* (Schfr.), Elateridae (adult), of the Coleoptera studied, were both the *dorsal* (anterior) and *ventral* (posterior) *labral muscles*, 4 and 3 (figs. 68, 70), present. In

*Heteroderes nicholsi* Notman (adult) the *ventral muscle of the labrum*, 3 (fig. 74), arises laterally on the anterior region of the clypeus; this is an unusual point of origin for this muscle. In the larval *Parallelostethus attenuatus* (Say) there are posterior extensions of the anterior tentorial arms that provide the points of origin for the long labial muscles, 20 and 21 (figs. 72, 73).

In *Popillia japonica* Newman, Scarabaeidae (adult) (figs. 75, 76, 77), the labial muscles are absent and an unusual muscle in the labium, 39 (figs. 76, 77), is to be found only in this species.

The *levator muscle of the palpus*, 24 (figs. 88, 89), in *Macrobasis immaculata* (Say), Meloidae (adult), arises on the intralabial brace (IR).

In the larvae of *Mordella quadripunctata* (Say), Mordellidae, there is present a thin apodeme (fig. 97, AP) that arises medianly in the posterior region of the frons and extends deeply into the head cavity. All the labral, cibarial, dorsal pharyngeal muscles, and the *muscles of the hypopharyngeal bar Y*, 10, 10A, 10B (fig. 97), arise on this apodeme.

In the larva of *Cyllene robiniae* (Forst.), Cerambycidae, there is an unusual lobe that extends ventrally from the dorsal cibarial wall into the mouth region (figs. 102, 104); the lobe is furnished with muscle 40 and probably assists in some manner in food ingestion.

The epipharynx is large and unusual in structure in the adult *Apatides fortis* (Lec.), Bostrichidae (fig. 106, EP). In the larva of this species muscle 41 (fig. 108) is unusual in that it is not found in the other insects studied in this work.

In the adult of *Leptinotarsa decimlineata* (Say), Chrysomelidae, branch 10A of the *muscle of hypopharyngeal bar Y*, 10 (figs. 111, 112), arises on the posterior surface of the epistomal suture (fig. 111, ES). In this species the ventral part of the labial wall is connected with the anterior dorsal wall by means of an intralabial tendonous structure (fig. 112, TS).

The *dorsal muscle of the labium*, 20 (figs. 118, 119), in *Euparius marmoreus* (Oliv.), Platystomidae (adult), arises laterally in the posterior region of the head, posterior to the tentorium, and is inserted on the labium by means of a very long tendon.

In the larva of *Pantomorus leucoloma* Boh., Curculionidae, the resilient median process (fig. 127, ME) that extends posteriorly from the dorsal margin of the labrum probably does the work of a muscle in assisting in the return of the labrum to its resting position after the *ventral muscle of the labrum*, 3, relaxes.

Further investigations are necessary to determine the nature of the complete act of the ingestion of food by chewing insects. The facts presented in this paper indicate, however, that the cibarial, pharyngeal, and hypopharyngeal muscles, which are powerfully developed in many species, play an important part in ingestion. The action of these muscles is undoubtedly supplemented by that of the labial muscles to a varied degree depending on the species.



## MUSCLES CONSIDERED IN THIS STUDY

1. *Compressor muscle of the labrum.*
2. *Dilator muscle group of the labrum.*
3. *Ventral (posterior) muscle of the labrum.*
4. *Dorsal (anterior) muscle of the labrum.*
- 5, 6, 7. *Dorsal dilator muscles of the cibarium.*
8. *Dorsal dilator muscle of the cibarium.*
9. *Dorsal dilator muscle of the anterior region of the pharynx.*
10. *Muscle of hypopharyngeal bar Y.*
11. *Dorsal dilator muscle of the pharynx.*
- 11A. *Dorsal dilator muscle of the pharynx.*
12. *Compressor muscle group of the cibarium.*
13. *Compressor muscles of the anterior region of the cibarium.*
14. *Hypopharyngeal muscle of the mandible.*
15. *Anterior dorsal dilator muscle of the salivarium.*
16. *Dorsal salivary cup muscle.*
17. *Anterior salivary cup muscle.*
18. *Lateroventral salivary cup muscle.*
19. *Muscle of the hypopharynx.*
20. *Dorsal (anterior) muscle of the labium.*
21. *Ventral (posterior) muscle of the labium.*
- 21A. *Muscle of the labium.*
22. *Muscle of the prementum 2.*
- 22A. *Muscle of the prementum 1.*
23. *Depressor muscle of the labial palpus.*
24. *Levator muscle of the labial palpus.*
25. *Muscle of the labial palpus.*
26. *Muscle of the labial palpus.*
27. *Muscle of the labial palpus.*
28. *Flexor muscle of the glossa.*
29. *Flexor muscle of the paraglossa.*
30. *Ventral dilator muscle of the pharynx.*
31. *Lateral dilator muscles of the pharynx.*
32. *Dorsal appressor muscle group of the cibarium.*
33. *Muscles of the ventral wall of the cibarium.*
34. *Laterodorsal muscle of the cibarium.*
35. *Lateral muscle of the posterior cibarial region.*
- 36, 37, 38. *Maxillary muscles.*
39. *Median muscle of the labium.*
40. *Retractor muscle of anterior pharyngeal region.*
41. *Muscle of the labium.*

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# ABBREVIATIONS USED ON THE FIGURES

<i>AF</i> , antennal fossa.	<i>MT</i> , mentum.
<i>ANT</i> , antenna.	<i>MX</i> , maxilla.
<i>AT</i> , anterior tentorial arm.	<i>MXP</i> , maxillary palpus.
<i>CD</i> , cardo.	<i>NA</i> , nasale.
<i>CIB</i> , cibarium.	<i>O</i> , ocellus.
<i>CL</i> , clypeus.	<i>OE</i> , oesophagus.
<i>CPS</i> , cuspidate sclerite.	
<i>CS</i> , coronal suture.	
<i>E</i> , compound eye.	<i>PGL</i> , paraglossa.
<i>EP</i> , epipharynx.	<i>PH</i> , pharynx.
<i>ES</i> , epistomal suture.	<i>PMT</i> , prementum.
<i>FC</i> , frontal connective nerve.	<i>PSMT</i> , postmentum.
<i>FGN</i> , frontal ganglion.	<i>PT</i> , posterior tentorial pits.
<i>FR</i> , frons.	<i>PTN</i> , posttentorial structure.
<i>FS</i> , frontal suture.	
<i>GL</i> , glossa.	<i>RB</i> , resilient bar.
<i>GU</i> , gula.	<i>SB</i> , suboesophageal brace.
<i>HY</i> , hypopharynx.	<i>SC</i> , salivary cup.
<i>IR</i> , intralabial rod or brace.	<i>SD</i> , salivary duct.
<i>LB</i> , labium.	<i>SL</i> , suboral lobe.
<i>LBP</i> , labial palpus.	<i>SMT</i> , submentum.
<i>LIG</i> , ligula.	<i>SR</i> , sclerotized rod.
<i>LM</i> , labium.	<i>ST</i> , stomodaeum.
<i>M</i> , true mouth opening.	<i>T</i> , torus.
<i>MD</i> , mandible.	<i>TB</i> , tentorial bridge.
<i>ME</i> , median posterior extension.	<i>TN</i> , tentorium.
	<i>TS</i> , tendinous structure.
	<i>Y</i> , hypopharyngeal bar <i>Y</i> .

## EXPLANATION OF PLATES

### PLATE 1

1. *Periplaneta americana* L., Orthoptera, sagittal section of head slightly to the left of median plane.
- 1A. Same, diagrammatic detail of the relation of the *dorsal dilator muscle of the cibarium*, 8, to the *dorsal muscle of the labrum*, 4.
2. Same, dorsal view of head with part of head wall removed to expose muscles.
3. Same, ventral view of labium and posterior head region with part of integument removed to expose muscles.
- 3A. Same, diagrammatic detail of relationship of the muscles of the labial palpus, 25, 26, and 27.

### PLATE 2

4. *Anisobasis maritima* Gené, Dermaptera, dorsal view of head with part of head wall removed to expose muscles.
5. Same, sagittal section of head slightly to the left of median plane.
6. Same, ventral view of head with part of integument removed to expose muscles.
7. *Corydalus cornutus* L., Neuroptera (adult), dorsal view of part of head with integument removed to expose muscles.
8. Same, sagittal section of head slightly to the left of median plane.
9. Same, ventral view of head with part of integument removed to expose muscles.

### PLATE 3

10. *Corydalus cornutus* L., Neuroptera (larva), dorsal view of head with part of integument removed to expose muscles.
11. Same, ventral view of head with part of integument removed to expose muscles.
12. Same, sagittal view of head slightly to the left of median plane.
13. *Sphecius speciosus* (Dru.), Hymenoptera (adult), lateral view of labium with part of integument removed to expose muscles and also portion of anterior tentorial arm with points of muscle origin.
14. Same, sagittal section of anterior (dorsal) head region slightly to the left of the median plane.
15. Same, dorsal view of anterior region of head with part of integument removed to expose muscles.
16. Same, ventral view of labium and tentorium with part of integument removed to expose muscles.

### PLATE 4

17. *Harpalus caliginosus* F., Carabidae (adult), dorsal view of head with part of integument removed to expose muscles.
18. Same, ventral view of labium with part of integument removed to expose muscles.

19. Same, sagittal section of head slightly to the left of median plane.
20. *Amara* sp., Carabidae (larva), ventral view of labium with part of integument removed to expose muscles.
21. Same, dorsal view of head with part of integument removed to expose muscles.
22. Same, sagittal section slightly to the left of median plane.

## PLATE 5

23. *Dineutes discolor* Aubé, Gyrinidae (adult), sagittal section of head slightly to the left of median plane.
24. Same, dorsal view of head with part of integument removed to expose muscles.
25. Same, ventral view of labium with part of integument removed to expose muscles.
26. *Dineutes* sp., Gyrinidae (larva), dorsal view of head with part of integument removed to expose muscles.
27. Same, ventral view of labium with part of integument removed to expose muscles.
28. Same, sagittal section of head slightly to the left of the median plane.

## PLATE 6

29. *Silpha americana* L., Silphidae (adult), dorsal view of head with part of integument removed to expose muscles.
30. Same, ventral view of head with part of integument removed to expose muscles.
31. Same, sagittal section of head slightly to the left of median plane.
32. *Silpha americana* L., Silphidae (larva), dorsal view of head with part of integument removed to expose muscles.
33. Same, ventral view of labium with part of integument removed to expose muscles.
34. Same, sagittal section of head slightly to the left of median plane.

## PLATE 7

35. *Sphaeridium scarabaeoides* L., Hydrophilidae (adult), dorsal view of head with part of integument removed to expose muscles.
36. Same, ventral view of head with part of integument removed to expose muscles.
37. Same, sagittal section of head slightly to the left of median plane.
38. *Sphaeridium bipustulatum* Fabr., Hydrophilidae (larva), dorsal view of head with part of integument removed to expose muscles.
39. Same, sagittal section of head slightly to the left of median plane.
40. Same, ventral view of labium with part of integument removed to expose muscles.
41. *Scotobates calcaratus* (Fab.), Tenebrionidae (adult), modified sagittal section of head slightly to the left of median plane.

## PLATE 8

42. *Scotobates calcaratus* (Fab.), Tenebrionidae (adult), ventral view of head with part of integument removed to expose muscles.



43. Same, dorsal view of head with part of integument removed to expose muscles.
44. *Scotobates calcaratus* (Fab.), Tenebrionidae (larva), dorsal view of head with part of integument removed to expose muscles.
45. Same, ventral view of anterior portion of head with part of integument removed to expose muscles.
46. Same, sagittal section of head slightly to the left of median plane.

## PLATE 9

47. *Byrrhus* sp., Byrrhidae (larva), anterior portion of head with part of integument removed to expose muscles.
48. Same, sagittal section of head slightly to the left of median plane.
49. Same, ventral view of head with part of integument removed to expose muscles.
50. *Nosodendron californicum* Horn, Nosodendridae (adult), ventral view of head with part of integument removed to expose muscles.
51. Same, dorsal view of head with part of integument removed to expose muscles.
52. Same, sagittal section of head slightly to the left of median plane.

## PLATE 10

53. *Nosodendron californicum* Horn, Nosodendridae (larva), dorsal view of head with part of integument removed to expose muscles.
54. Same, sagittal section of head slightly to the left of median plane.
55. Same, ventral view of head with part of integument removed to expose muscles.
56. *Helichus fastigiatus* (Say), Dryopidae (adult), dorsal view of head with part of integument removed to expose muscles.
57. Same, sagittal section of head slightly to the left of median plane.
58. Same, ventral view of head with part of integument removed to expose muscles.

## PLATE 11

59. *Ptilodactyla serricollis* (Say), Ptilodactylidae (larva), dorsal view of head with part of integument removed to expose muscles.
60. Same, ventral view of head with part of integument removed to expose muscles.
61. Same, sagittal section of head slightly to the left of median plane.
62. *Chauliognathus pennsylvanicus* (Deg.), Cantharidae (adult), sagittal section of head slightly to the left of median plane.
63. Same, dorsal view of head with part of integument removed to expose muscles.
64. Same, ventral view of head with part of integument removed to expose muscles.

## PLATE 12

65. *Chauliognathus pennsylvanicus* (Deg.), Cantharidae (larva), dorsal view of head with part of integument removed to expose muscles.
66. Same, ventral view of head with part of integument removed to expose muscles.

67. Same, sagittal section of head slightly to the left of median plane.
68. *Neotrichophorus carolinensis* (Schfr.), Elateridae (adult), sagittal section of head slightly to the left of median plane.
69. Same, ventral view of head with part of integument removed to expose muscles.
70. Same, dorsal view of head with part of integument removed to expose muscles.

## PLATE 13

71. *Parallelostethus attenuatus* (Say), Elateridae (larva), dorsal view of head with part of integument removed to expose muscles.
72. Same, ventral view of head with part of integument removed to expose muscles.
73. Same, sagittal section of head slightly to the left of median plane.
74. *Heteroderes nicholsi* Notman, Elateridae (adult), lateral view of labrum and clypeus with part of head wall removed to expose muscles.
75. *Popillia japonica* Newman, Scarabaeidae (adult), dorsal view of head with part of integument removed to expose muscles.
76. Same, sagittal section of head slightly to the left of median plane.

## PLATE 14

77. *Popillia japonica* Newman, Scarabaeidae (adult), ventral view of head with part of integument removed to expose muscles.
78. Same (larva), sagittal section of head slightly to the left of median plane.
79. Same, dorsal view of head with part of integument removed to expose muscles.
80. Same, ventral view of head with part of integument removed to expose muscles.
81. *Dermestes caninus* Germ., Dermestidae (adult), sagittal section of head slightly to the left of median plane.
82. Same, dorsal view of head with part of integument removed to expose muscles.

## PLATE 15

83. *Dermestes caninus* Germ., Dermestidae (adult), ventral view of head with part of integument removed to expose muscles.
84. Same, sagittal section of head slightly to the left of median plane.
85. Same, dorsal view of anterior portion of head with part of integument removed to expose muscles.
86. Same, ventral view of head with part of integument removed to expose muscles.
87. *Macrobasis immaculata* (Say), Meloidae (adult), dorsal view of head with part of integument removed to expose muscles.
88. Same, sagittal section of head slightly to the left of median plane.

## PLATE 16

89. *Macrobasis immaculata* (Say), Meloidae (adult), ventral view of head with part of integument removed to expose muscles.
90. *Zonabris phalerata* (Pall.), Meloidae (larva), dorsal view of head with part of integument removed to expose muscles.

91. Same, sagittal section of head slightly to the left of median plane.
92. Same, ventral view of head with part of integument removed to expose muscles.
93. *Mordella quadripunctata* (Say), Mordellidae (adult), sagittal section of head slightly to the left of median plane.
94. Same, dorsal view of head with part of the integument removed to expose muscles.

## PLATE 17

95. *Mordella quadripunctata* (Say), Mordellidae (adult), ventral view of head with part of integument removed to expose muscles.
96. Same (larva), dorsal view of head with part of integument removed to expose muscles.
97. Same, sagittal section of head slightly to the left of median plane.
98. Same, ventral view of head with part of integument removed to expose muscles.
99. *Cyllene robiniae* (Forst.), Cerambycidae (adult), sagittal section of head slightly to the left of median plane.

## PLATE 18

100. *Cyllene robiniae* (Forst.), Cerambycidae (adult), dorsal view of head with part of integument removed to expose muscles.
101. Same, ventral view of head with part of integument removed to expose muscles.
102. Same (larva), dorsal view of head with part of integument removed to expose muscles.
103. Same, ventral view of head with part of integument removed to expose muscles.
104. Same, sagittal section of head slightly to the left of median plane.

## PLATE 19

105. *Apatides fortis* (Lec.), Bostrichidae (adult), dorsal view of head with part of integument removed to expose muscles.
106. Same, sagittal section of head slightly to the left of median plane.
107. Same, ventral view of head with part of integument removed to expose muscles.
108. Same (larva), sagittal section of head slightly to the left of median plane.
109. Same, dorsal view of head with part of integument removed to expose muscles.

## PLATE 20

110. *Apatides fortis* (Lec.), Bostrichidae (larva), ventral view of portion of head with part of integument removed to expose muscles.
111. *Leptinotarsa decimlineata* (Say), Chrysomelidae (adult), dorsal view of head with part of integument removed to expose muscles.
112. Same, sagittal section of head slightly to the left of median plane.
113. Same, ventral view of portion of head with part of integument removed to expose muscles.
114. Same (larva), sagittal section of head slightly to the left of median plane.

## PLATE 21

115. *Leptinotarsa decimlineata* (Say), Chrysomelidae (larva), dorsal view of head with part of integument removed to expose muscles.
116. Same, ventral view of head with part of integument removed to expose muscles.
117. *Euparius marmoreus* (Oliv.), Platystomidae (adult), dorsal view of head with part of integument removed to expose muscles.
118. Same, sagittal section of head slightly to the left of median plane.
119. Same, ventral view of anterior portion of head with part of integument removed to expose muscles.
120. Same (larva), dorsal view of head with part of integument removed to expose muscles.

## PLATE 22

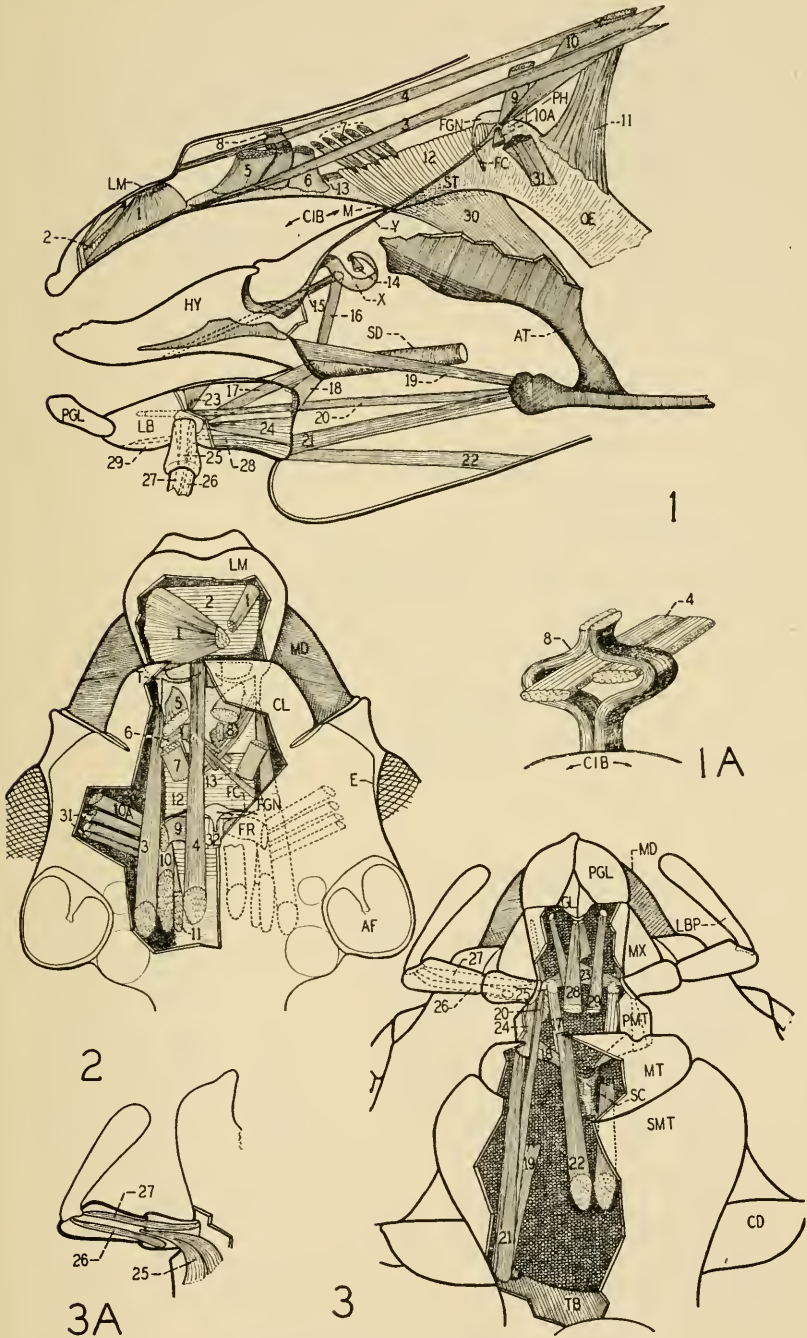
121. *Euparius marmoreus* (Oliv.), Platystomidae (larva), sagittal section of head slightly to the left of median plane.
122. Same, ventral view of head with part of integument removed to expose muscles.
123. *Pantomorus godmani* (Crotch), Curculionidae (adult), sagittal section of head slightly to the left of median plane.
124. Same, dorsal view of head with part of integument removed to expose muscles.
125. Same, ventral view of anterior portion of head with part of integument removed to expose muscles.

## PLATE 23

126. *Pantomorus leucoloma* Boh., Curculionidae (larva), dorsal view of anterior region of head with part of integument removed to expose muscles.
127. Same, sagittal section of head slightly to the left of median plane.
128. Same, ventral view of head with part of integument removed to expose muscles.
129. *Hylecoetus lugubris* Say, Lymexylidae (adult), dorsal view of head with part of integument removed to expose muscles.

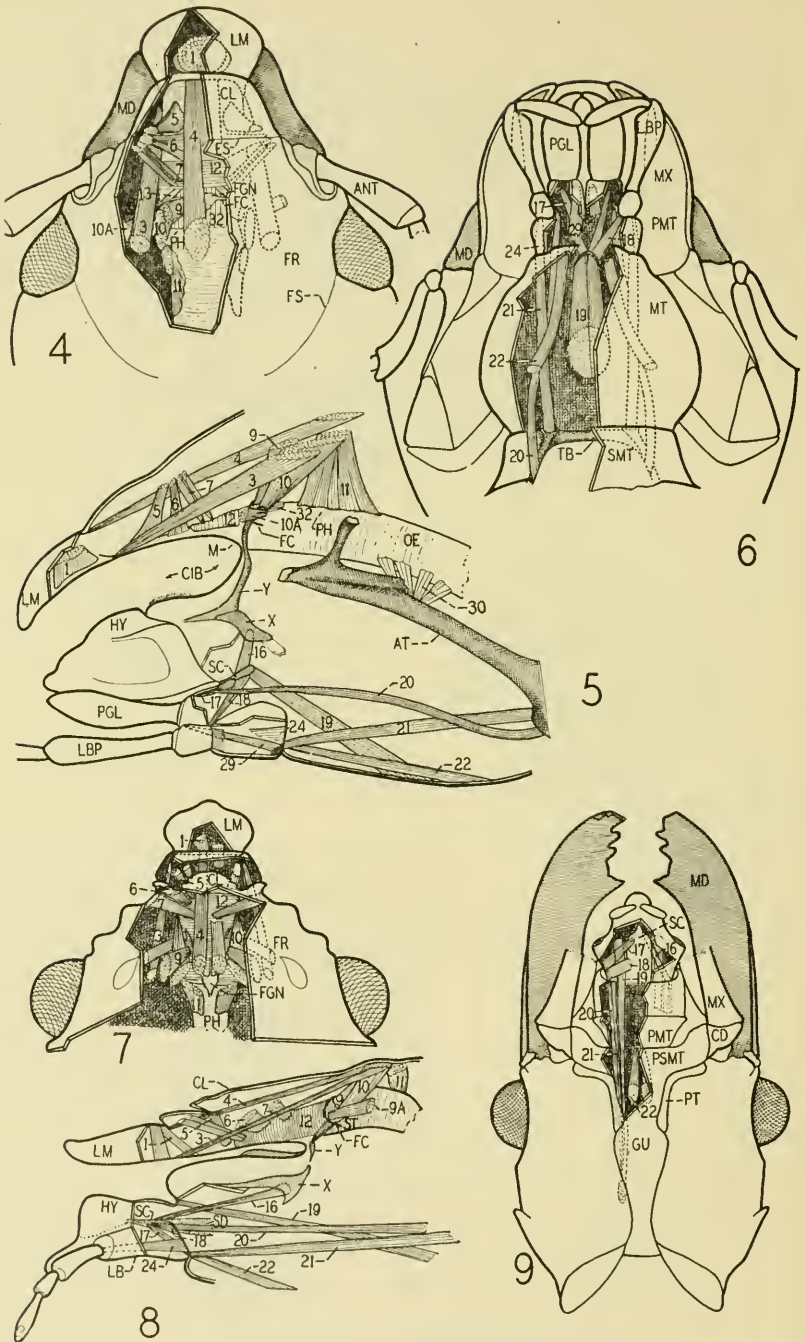
## PLATE 24

130. *Hylecoetus lugubris* Say, Lymexylidae (adult), sagittal section of head slightly to the left of median plane.
131. Same, ventral view of head with part of integument removed to expose muscles.
132. Same (larva), sagittal section of head slightly to the left of median plane.
133. Same, dorsal view of anterior portion of head with part of integument removed to expose muscles.
134. Same, ventral view of head with part of integument removed to expose muscles.



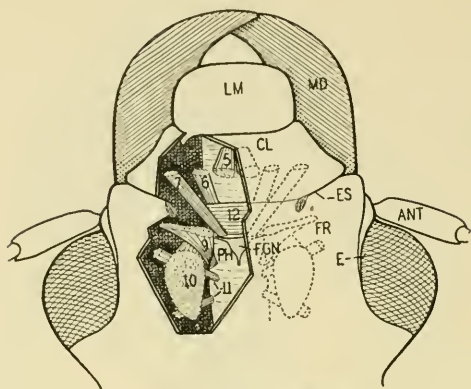
MUSCULATURE OF COLEOPTERA  
(For explanation of plate see page 37.)



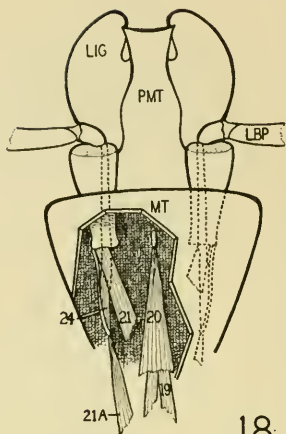


MUSCULATURE OF COLEOPTERA  
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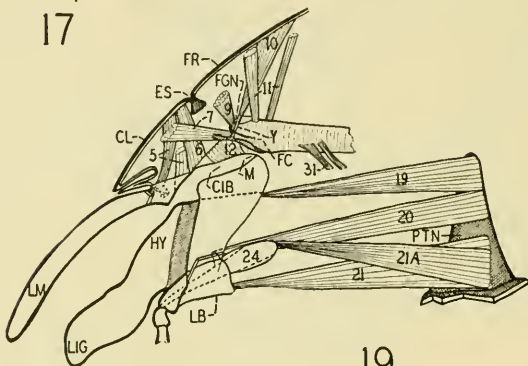




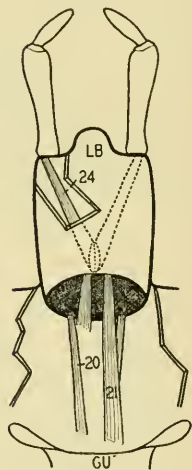
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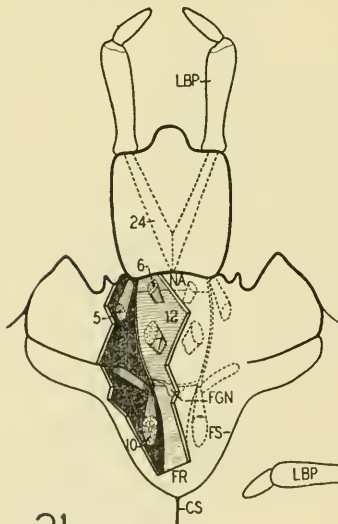
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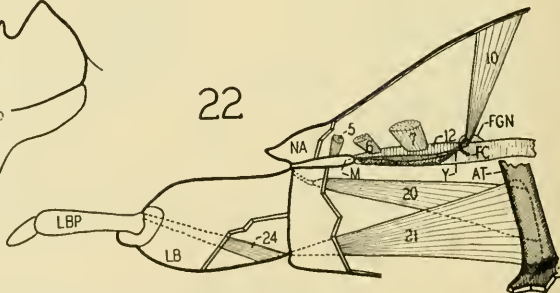
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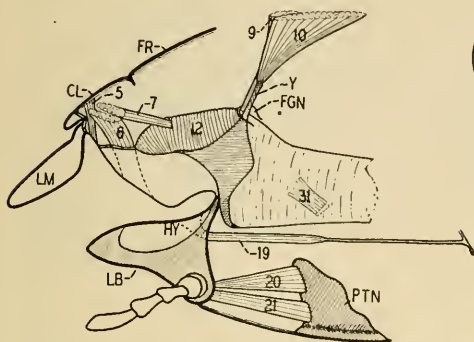
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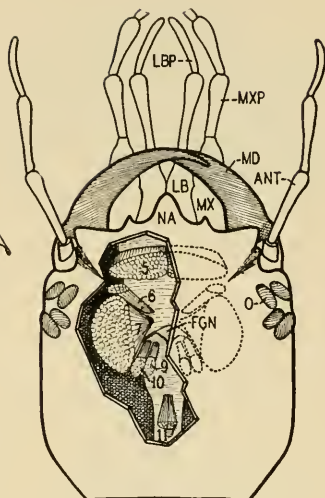
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## MUSCULATURE OF COLEOPTERA

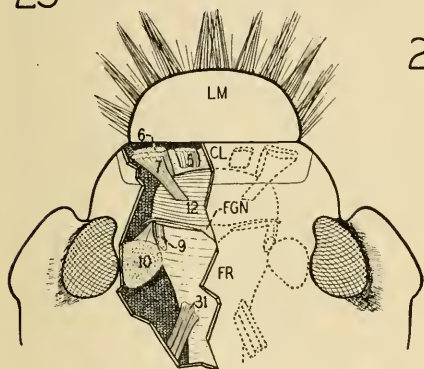
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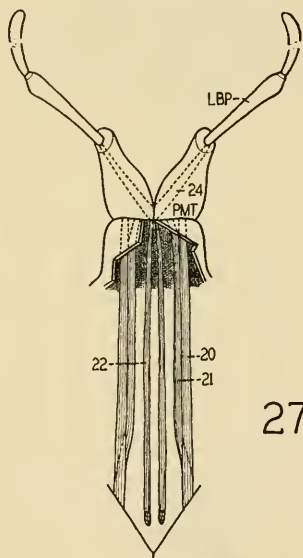
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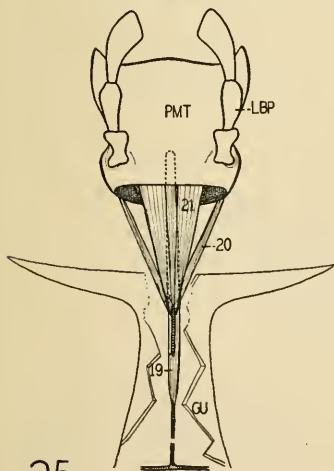
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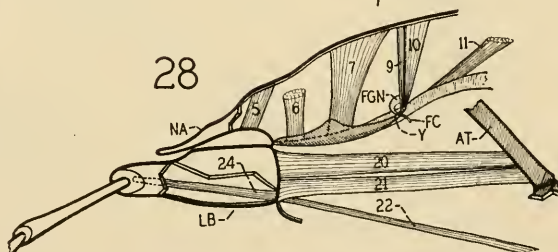
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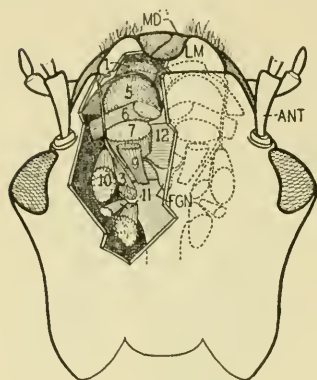


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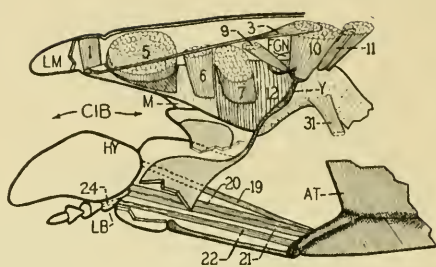
## MUSCULATURE OF COLEOPTERA

(For explanation of plate see page 38.)

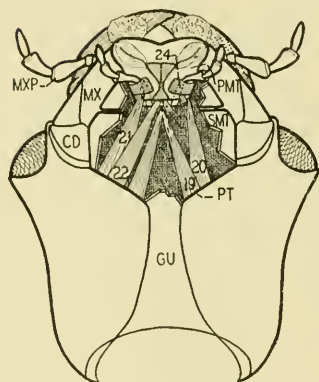




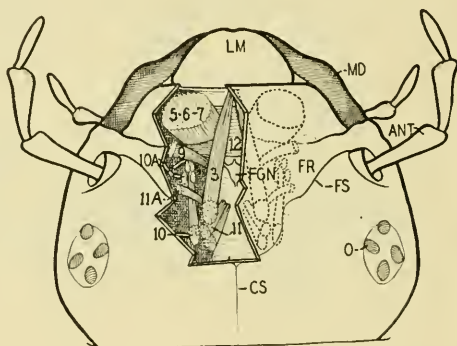
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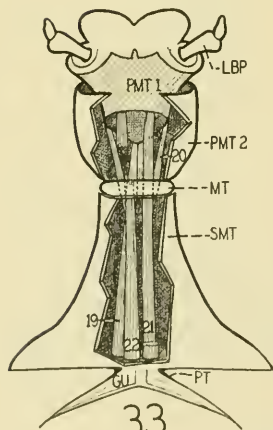
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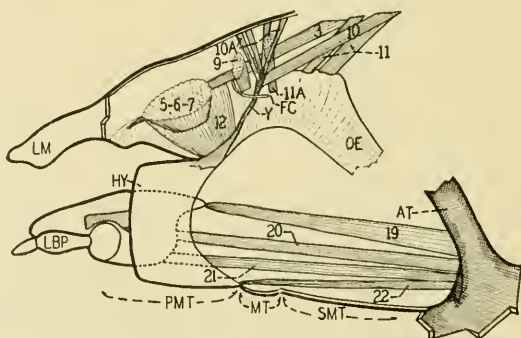
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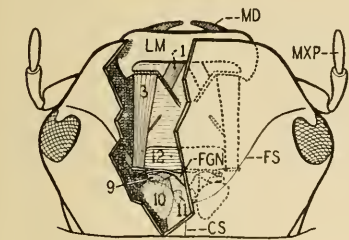


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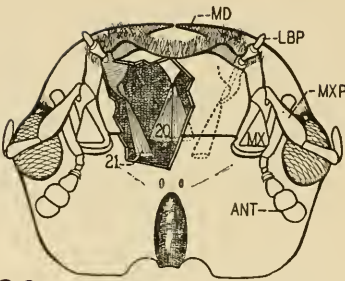


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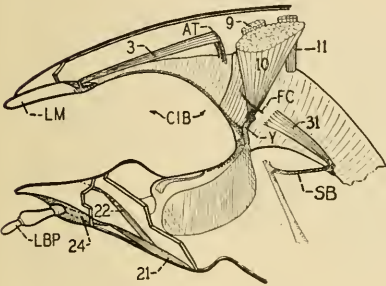




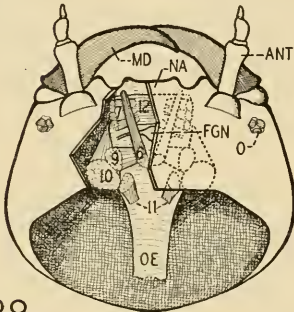
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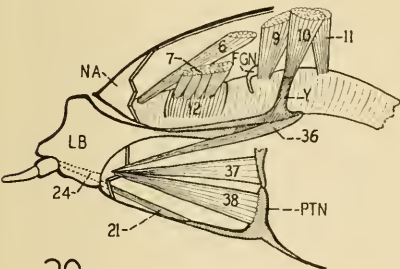
36



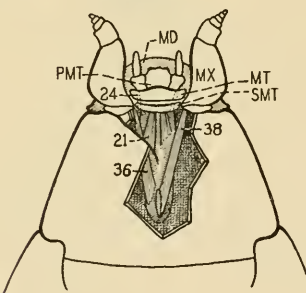
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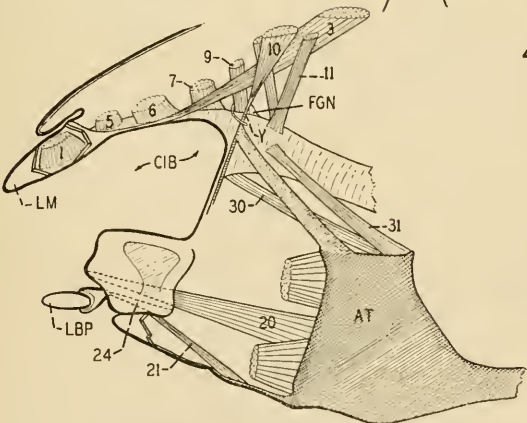
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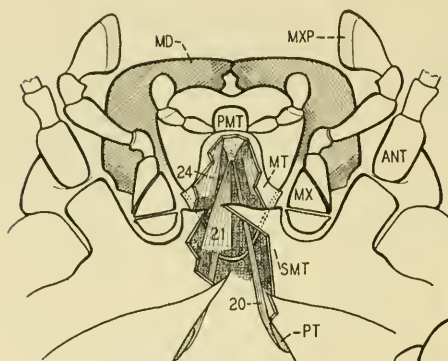
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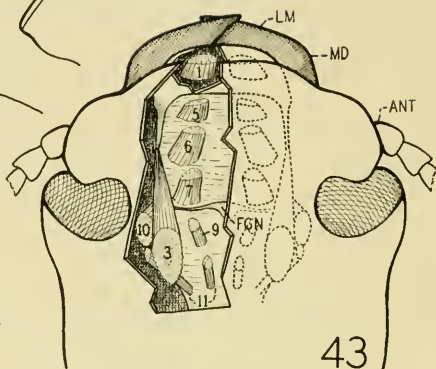
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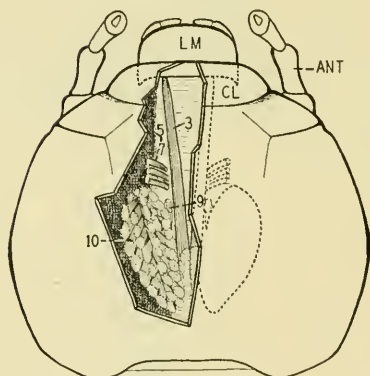
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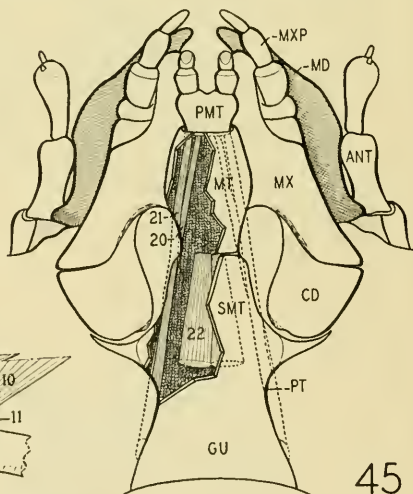
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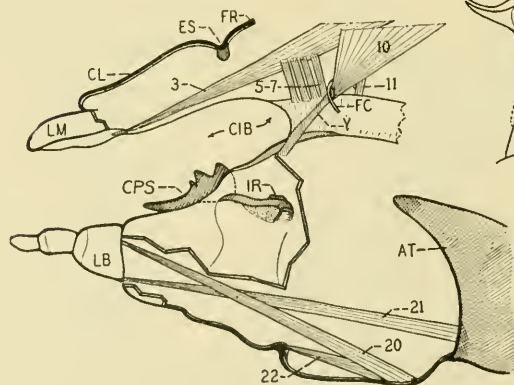
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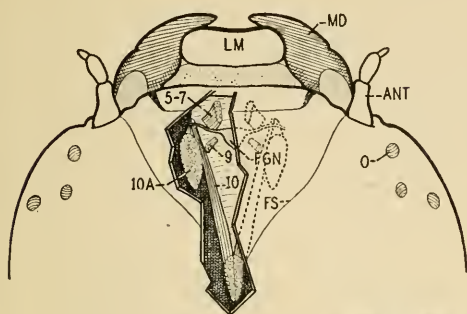


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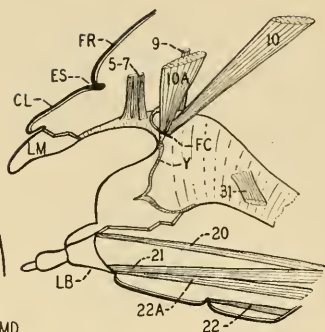


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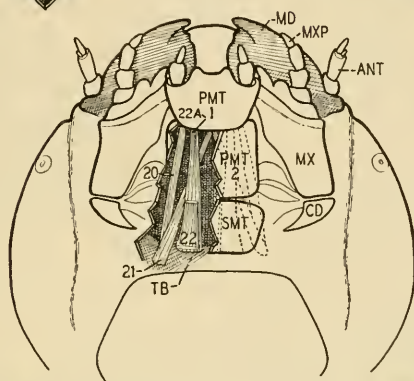
MUSCULATURE OF COLEOPTERA  
(For explanation of plate see pages 38-39.)



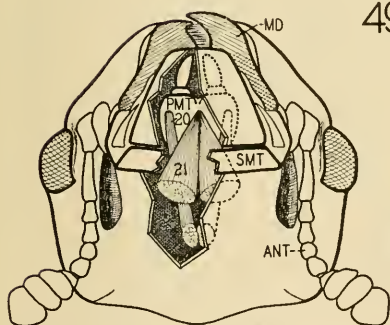
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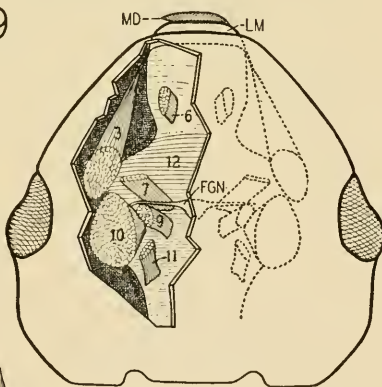
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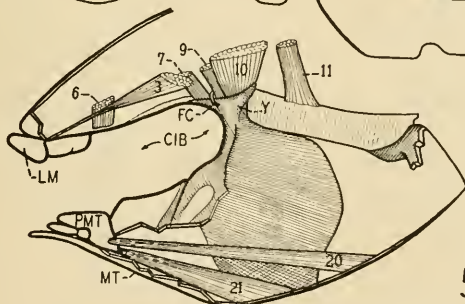
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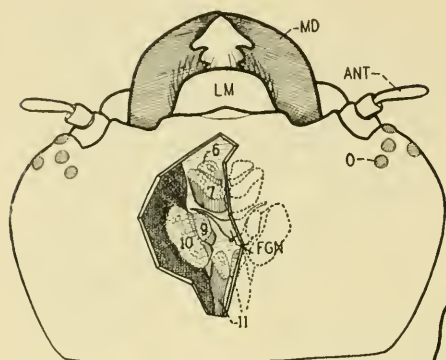


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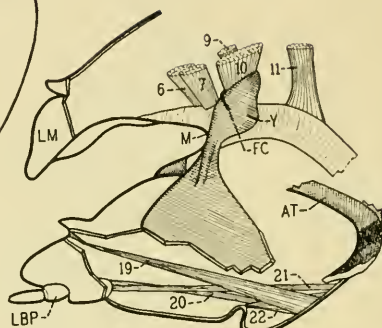


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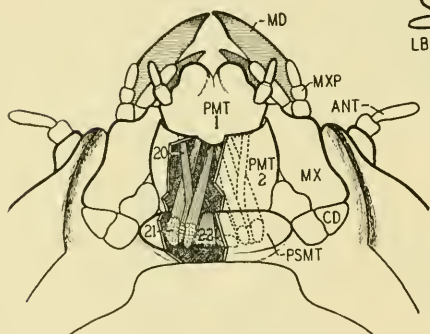
MUSCULATURE OF COLEOPTERA  
(For explanation of plate see page 39.)



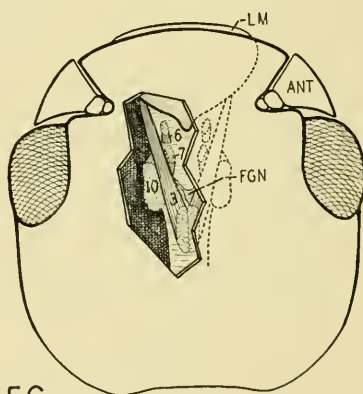
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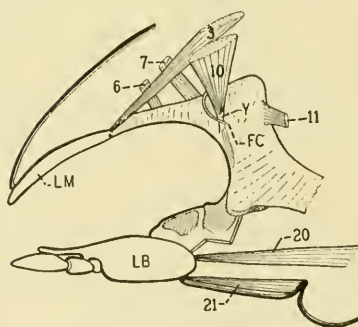
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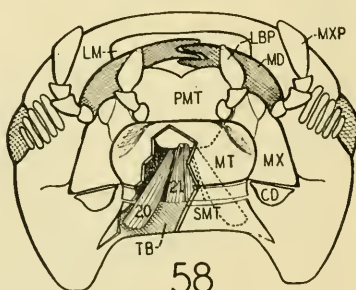
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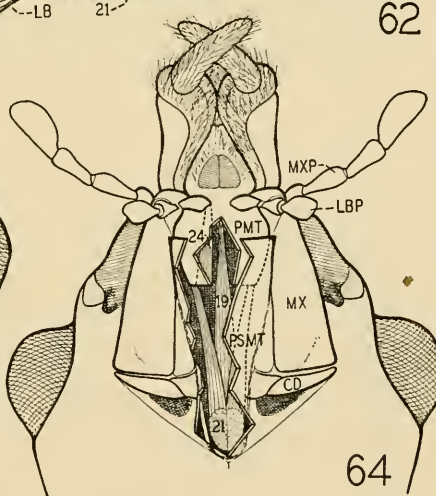
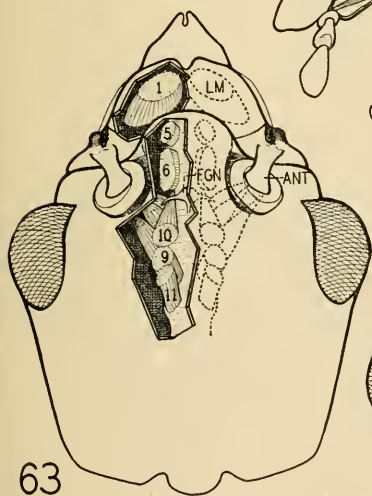
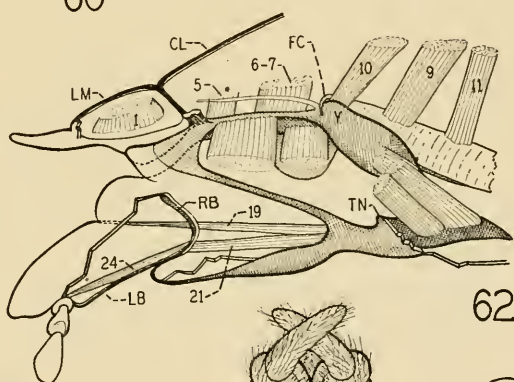
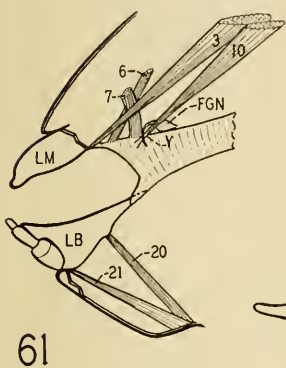
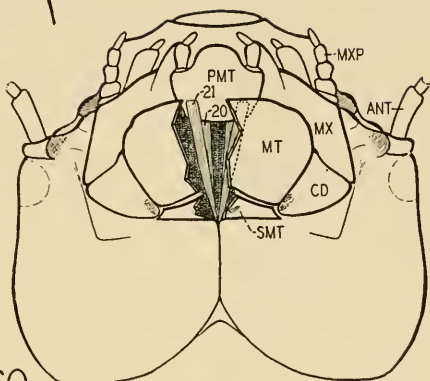
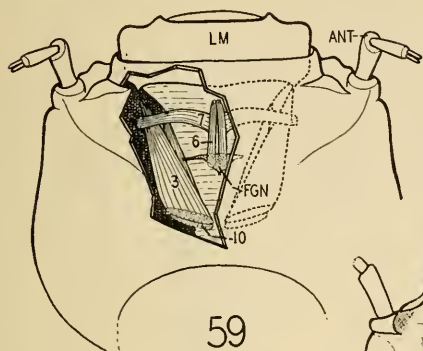


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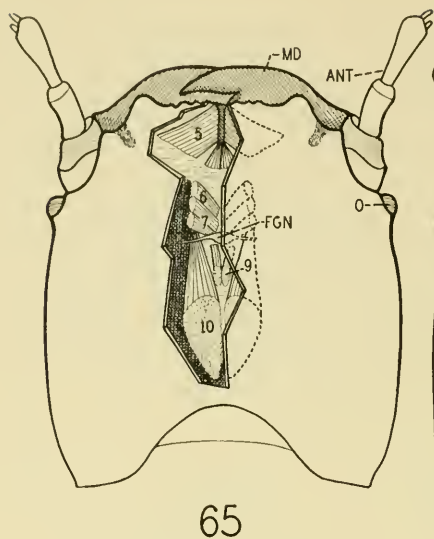


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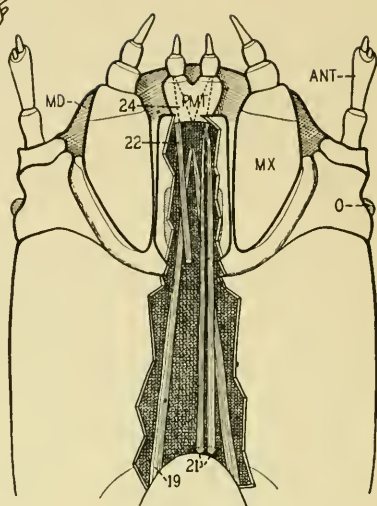




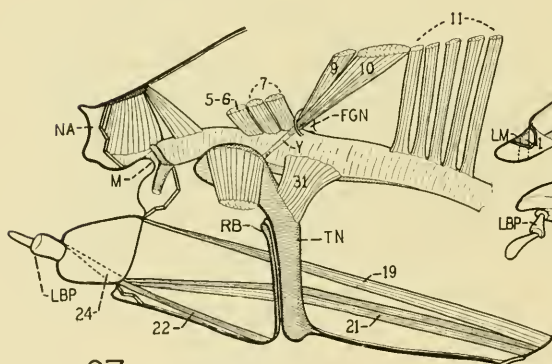




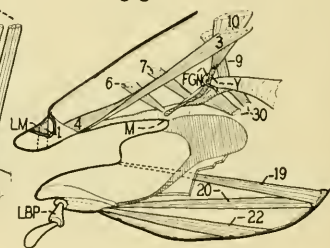
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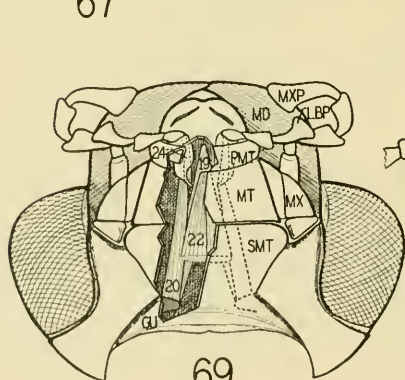
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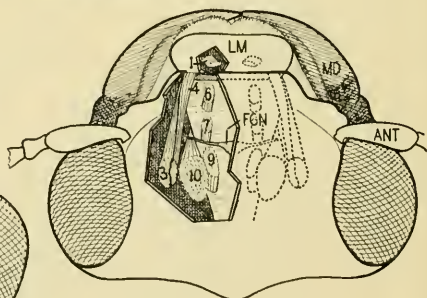
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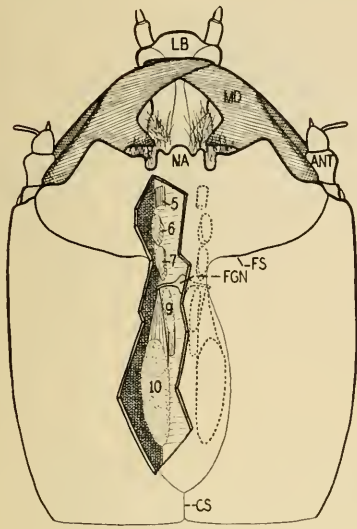
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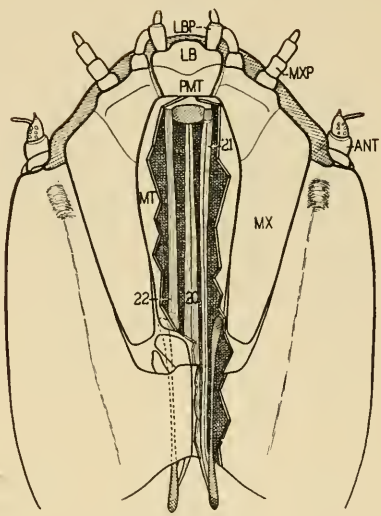
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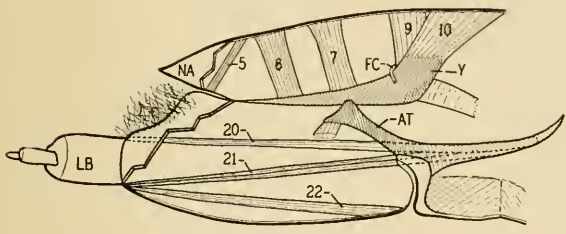
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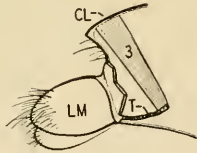
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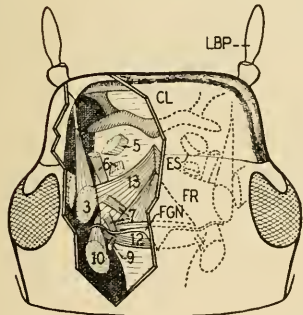
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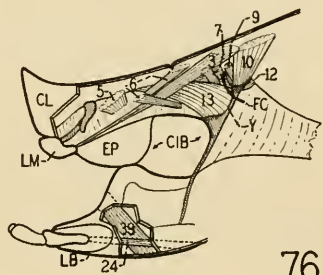
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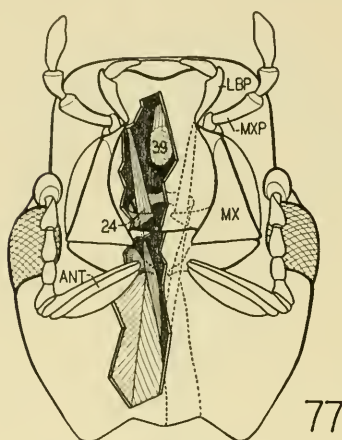
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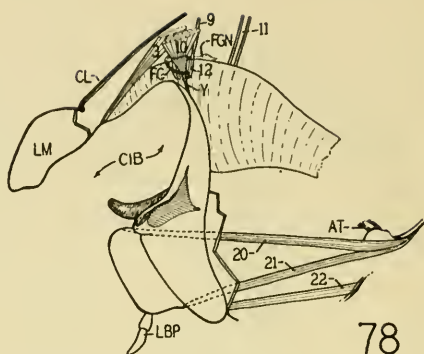
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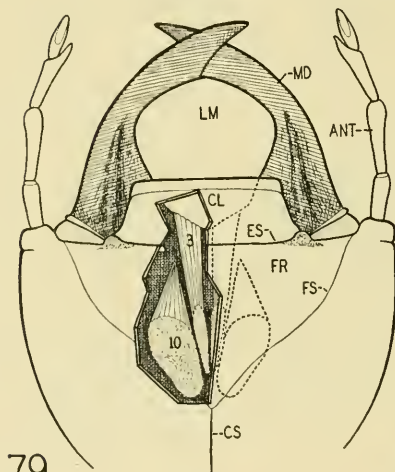
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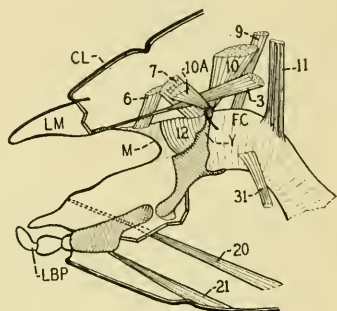
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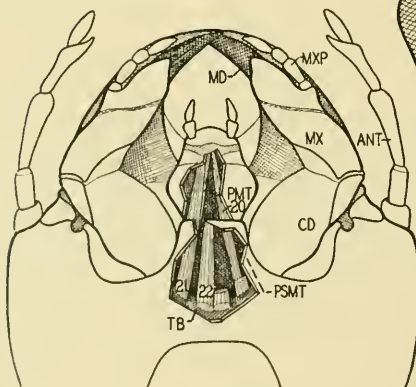
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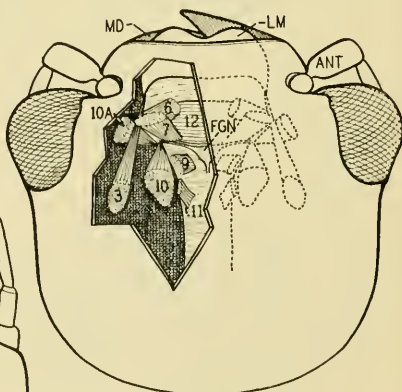
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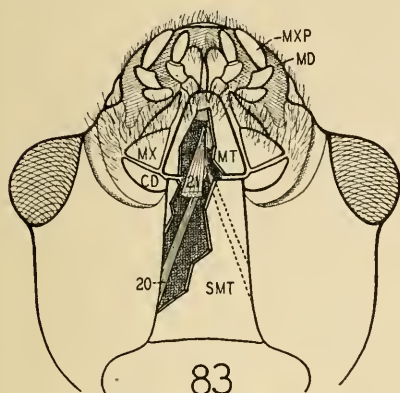
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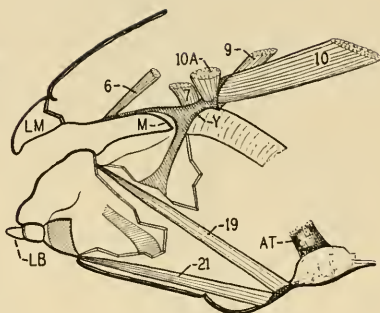
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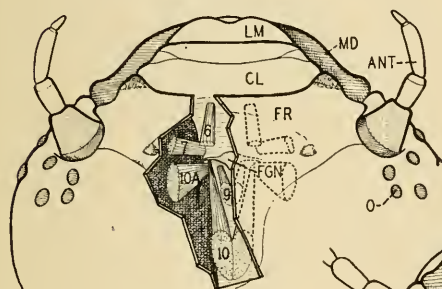
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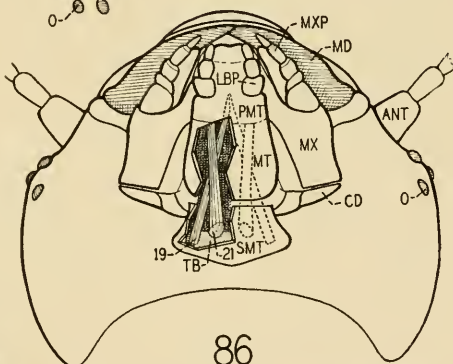
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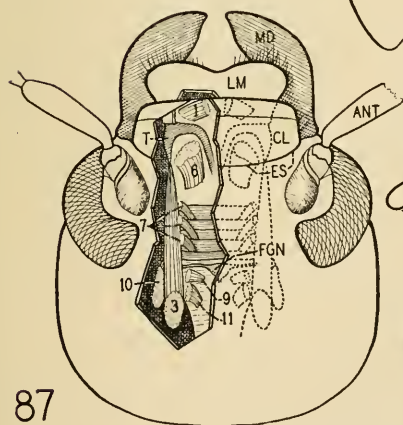
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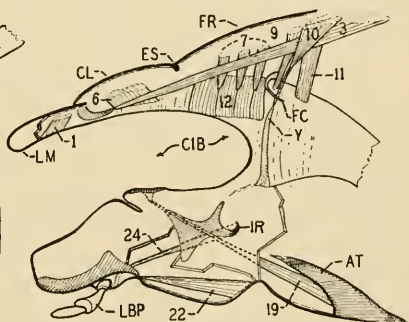
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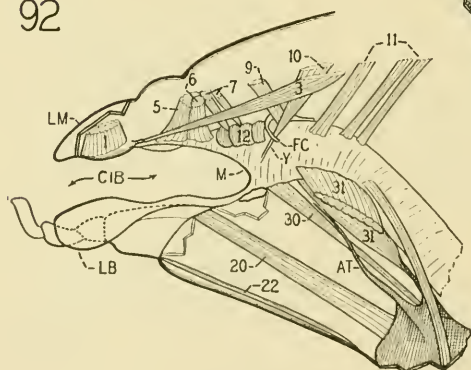
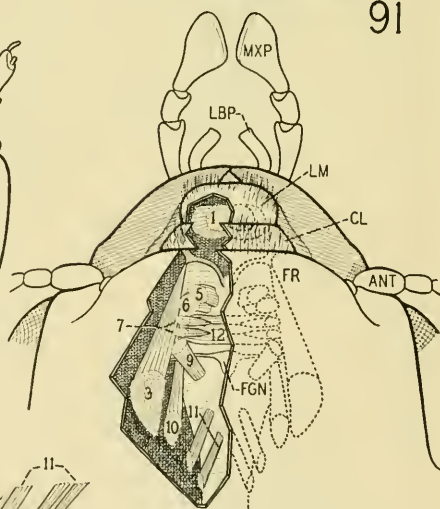
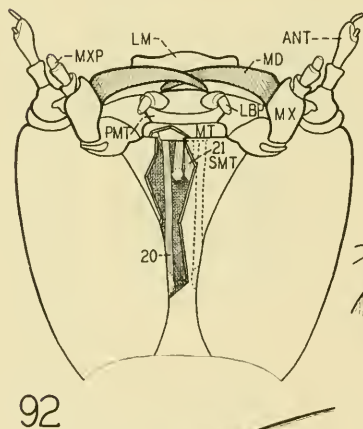
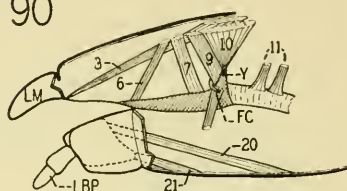
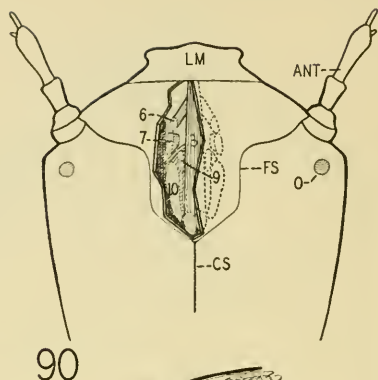
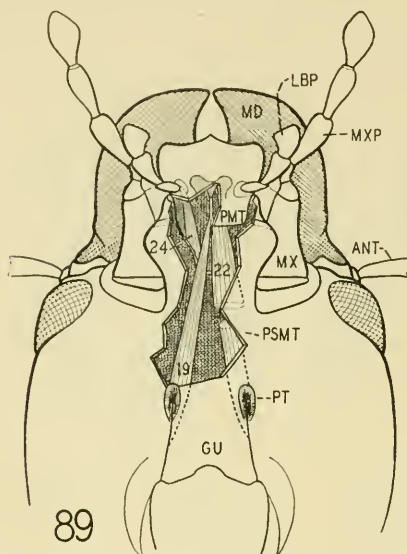


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88

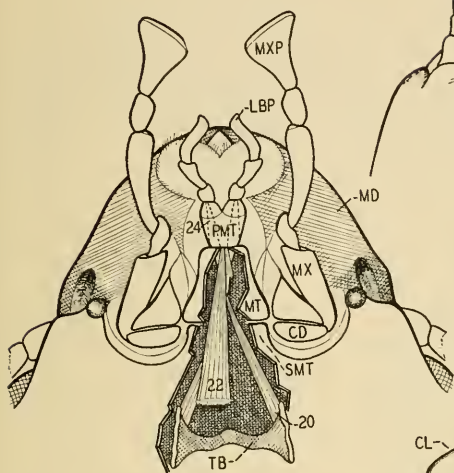




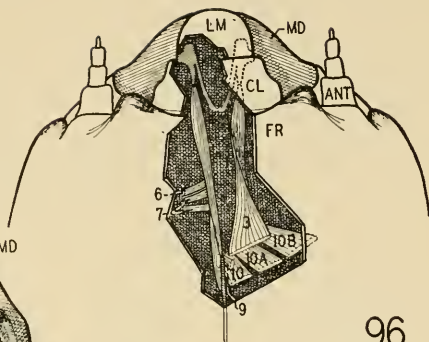
## MUSCULATURE OF COLEOPTERA

(For explanation of plate see pages 40-41.)

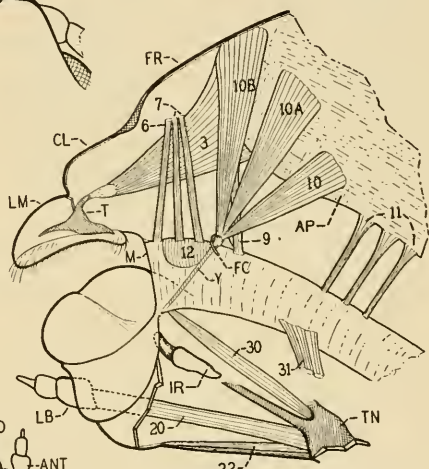




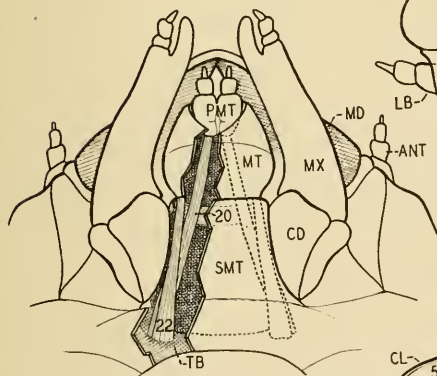
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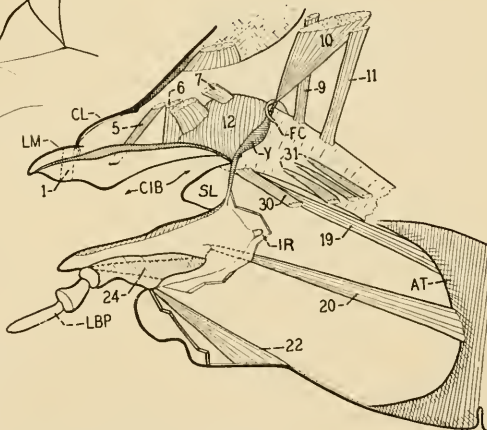
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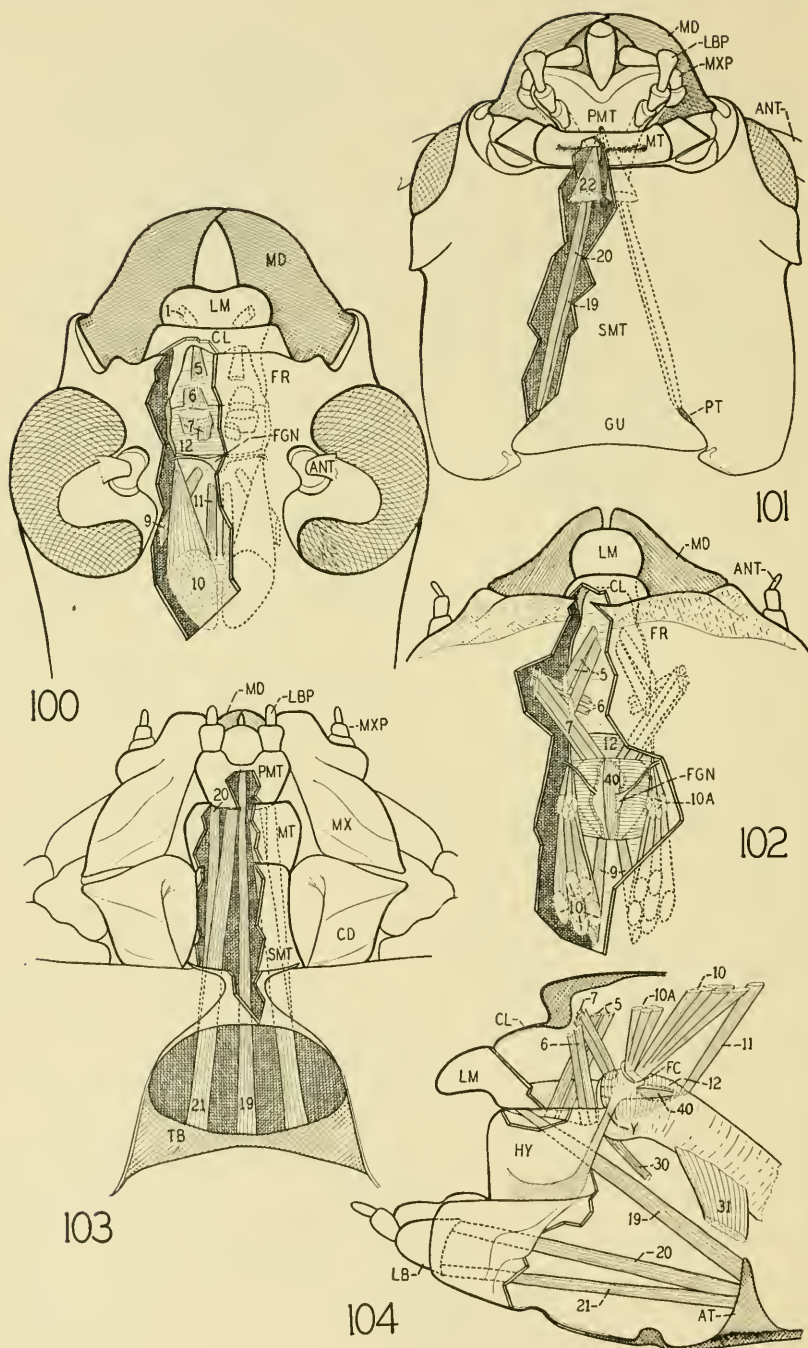
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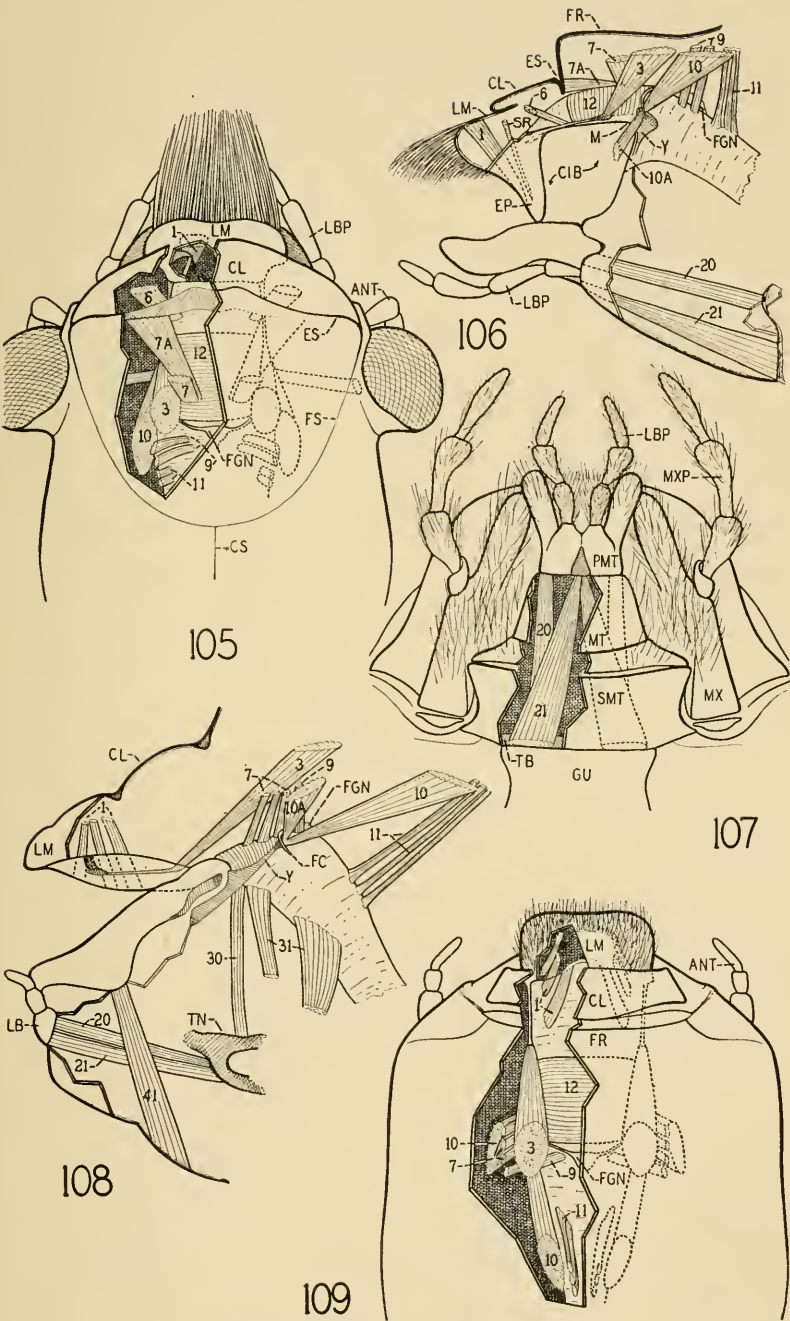
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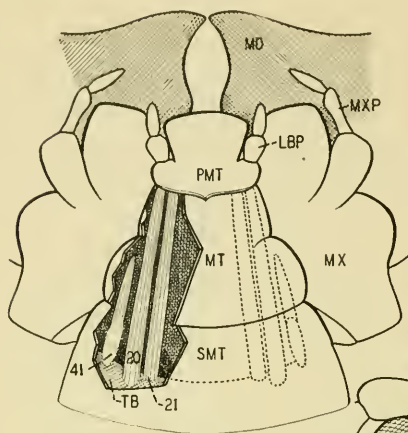
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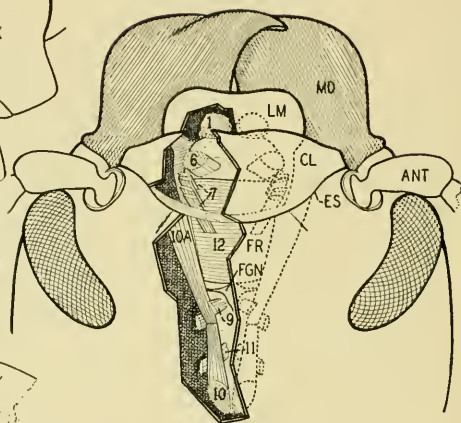
MUSCULATURE OF COLEOPTERA  
(For explanation of plate see page 41.)



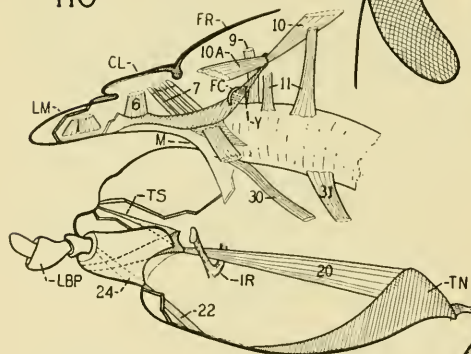
MUSCULATURE OF COLEOPTERA  
(For explanation of plate see page 41.)



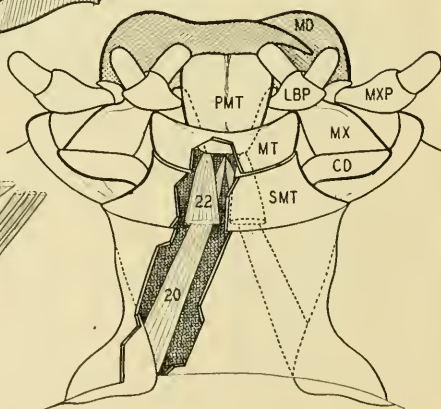
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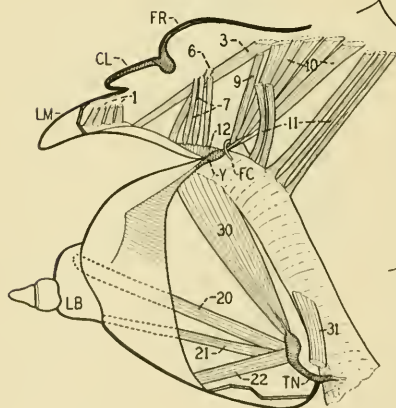
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112

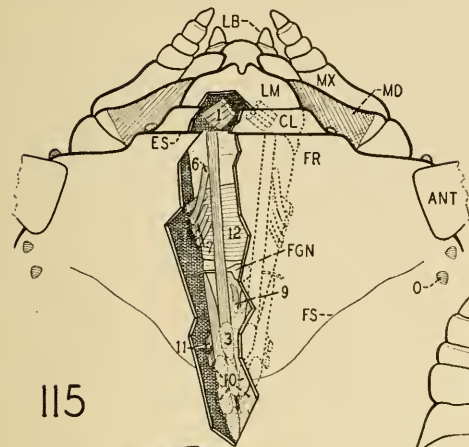


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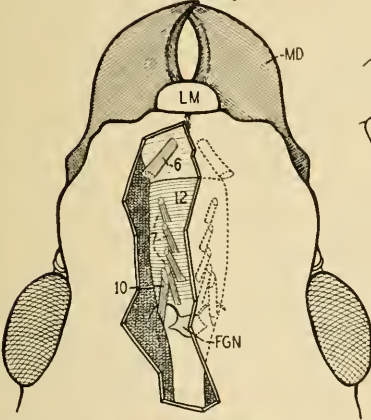


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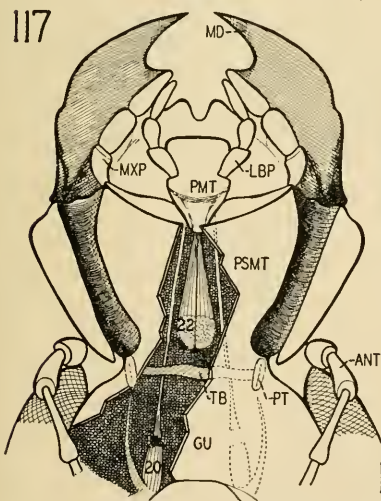




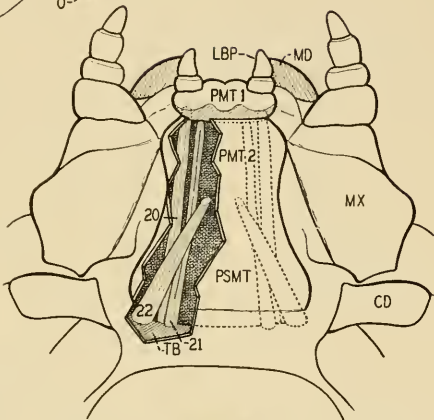
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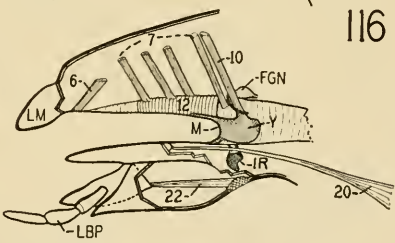
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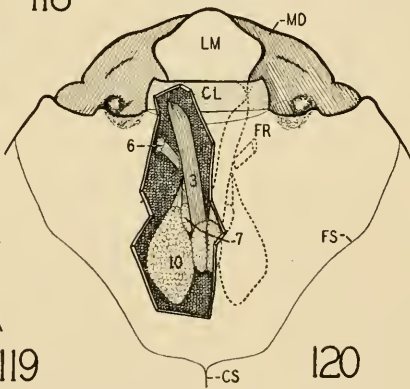
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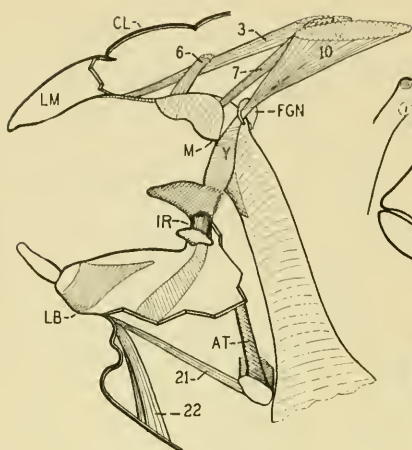


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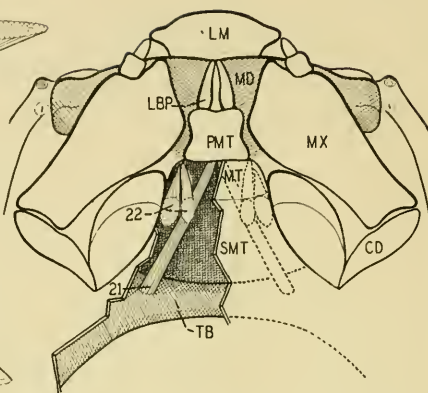


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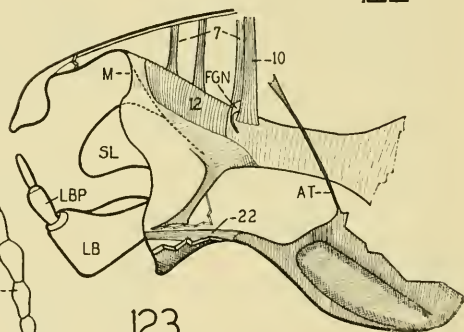




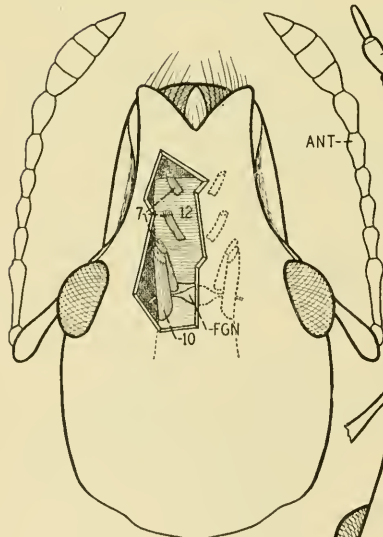
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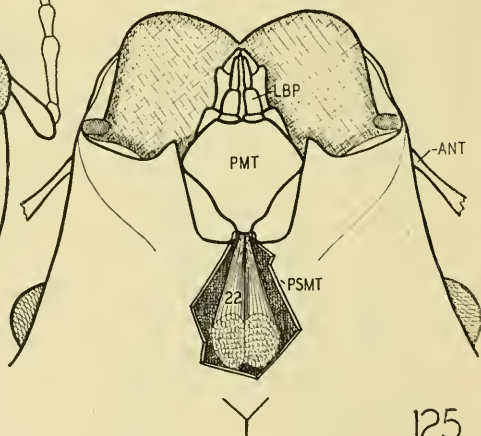
122



123

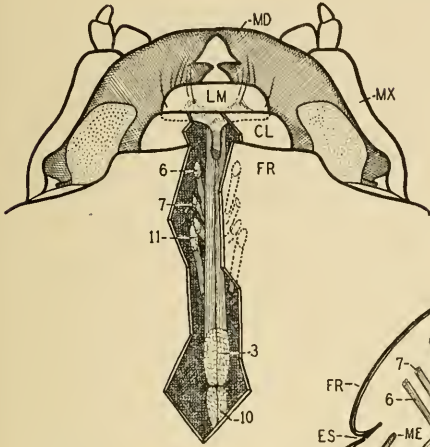


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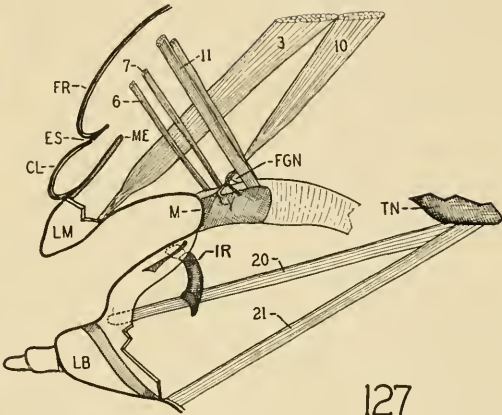


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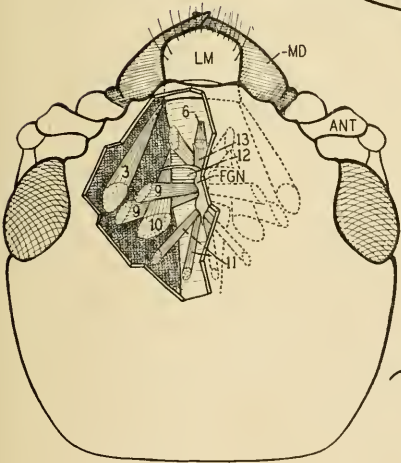
MUSCULATURE OF COLEOPTERA  
(For explanation of plate see page 42.)



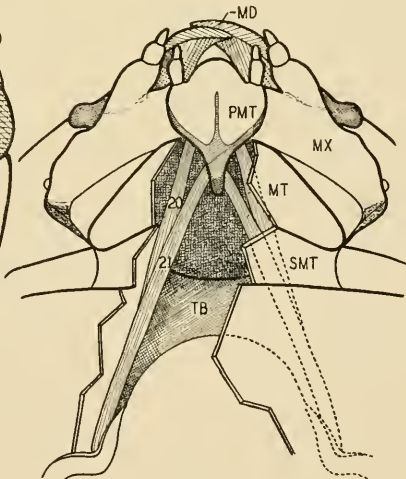
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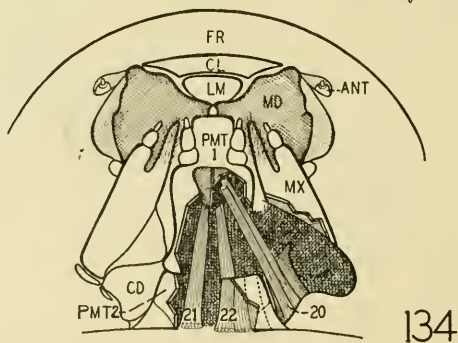
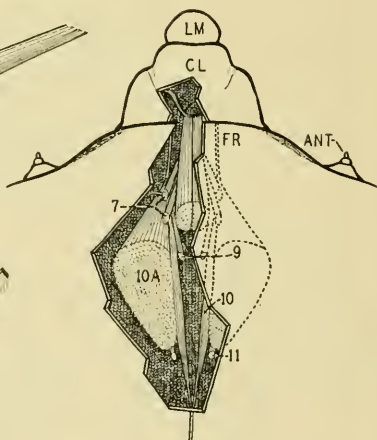
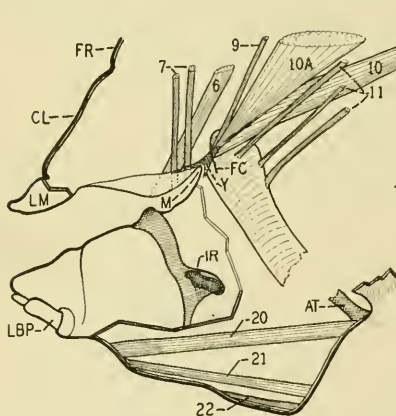
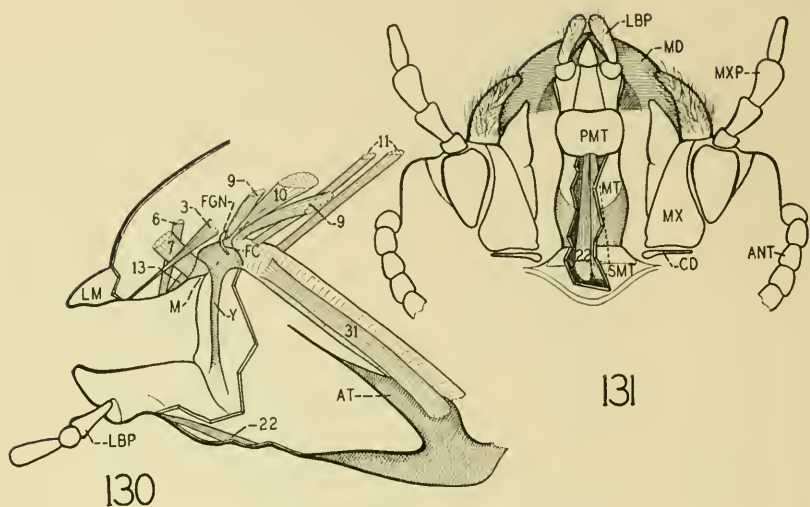
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MUSCULATURE OF COLEOPTERA  
(For explanation of plate see page 42.)







SMITHSONIAN MISCELLANEOUS COLLECTIONS  
VOLUME 103, NUMBER 8

# THE 1914 TESTS OF THE LANGLEY "AERODROME"

BY  
C. G. ABBOT  
Secretary, Smithsonian Institution



(PUBLICATION 3699)

CITY OF WASHINGTON  
PUBLISHED BY THE SMITHSONIAN INSTITUTION  
OCTOBER 24, 1942



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OCTOBER 24, 1942

*The Lord Baltimore Press*  
BALTIMORE, MD., U. S. A.

## THE 1914 TESTS OF THE LANGLEY "AERODROME" <sup>1</sup>

By C. G. ABBOT

*Secretary, Smithsonian Institution*

NOTE—This paper has been submitted to Dr. Orville Wright, and under date of October 8, 1942, he states that the paper as now prepared will be acceptable to him if given adequate publication.

It is everywhere acknowledged that the Wright brothers were the first to make sustained flights in a heavier-than-air machine at Kitty Hawk, North Carolina, on December 17, 1903.

Mainly because of acts and statements of former officers of the Smithsonian Institution, arising from tests made with the reconditioned Langley plane of 1903 at Hammondsport, New York, in 1914, Dr. Orville Wright feels that the Institution adopted an unfair and injurious attitude. He therefore sent the original Wright Kitty Hawk plane to England in 1928. The nature of the acts and statements referred to are as follows:

In March 1914, Secretary Walcott contracted with Glenn H. Curtiss to attempt a flight with the Langley machine. This action seems ill considered and open to criticism. For in January 1914, the United States Court of Appeals, Second Circuit, had handed down a decision recognizing the Wrights as "pioneers in the practical art of flying with heavier-than-air machines" and pronouncing Glenn H. Curtiss an infringer of their patent. Hence, in view of probable further litigation, the Wrights stood to lose in fame and revenue and Curtiss stood to gain pecuniarily, should the experiments at Hammondsport indicate that Langley's plane was capable of sustained flight in 1903, previous to the successful flights made December 17, 1903, by the Wrights at Kitty Hawk, N. C.

The machine was shipped to Curtiss at Hammondsport, N. Y. in April. Dr. Zahm, the Recorder of the Langley Aerodynamical Laboratory and expert witness for Curtiss in the patent litigation, was at Hammondsport as official representative of the Smithsonian Institution during the time the machine was being reconstructed and tested. In the reconstruction the machine was changed from what it was in 1903 in a number of particulars as given in Dr. Wright's

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<sup>1</sup> For an account of early Langley and Wright aeronautical investigations, see Smithsonian Report for 1900 and *The Century Magazine* of September 1908.



list of differences which appears later in this paper. On the 28th of May and the 2d of June, 1914, attempts to fly were made. After acquiring speed by running on hydroplane floats on the surface of Lake Keuka the machine lifted into the air several different times. The longest time off the water with the Langley motor was approximately five seconds. Dr. Zahm stated that "it was apparent that owing to the great weight which had been given to the structure by adding the floats it was necessary to increase the propeller thrust". So no further attempts were made to fly with the Langley 52 HP engine.

It is to be regretted that the Institution published statements repeatedly <sup>2</sup> to the effect that these experiments of 1914 demonstrated that Langley's plane of 1903 without essential modification was the first heavier-than-air machine capable of maintaining sustained human flight.

As first exhibited in the United States National Museum, January 15, 1918, the restored Langley plane of 1903 bore the following label:

THE ORIGINAL, FULL-SIZE  
LANGLEY FLYING MACHINE, 1903

For this simple label others were later substituted containing the claim that Langley's machine "was the first man-carrying aeroplane in the history of the world capable of sustained free flight."

Though the matter of the label is not now an issue, it seems only fair to the Institution to say that in September 1928, Secretary Abbot finally caused the label of the Langley machine to be changed to read simply as follows:

LANGLEY AERODROME  
THE ORIGINAL SAMUEL PIERPONT LANGLEY  
FLYING MACHINE OF 1903, RESTORED.

Deposited by  
The Smithsonian Institution

301,613

This change has frequently been overlooked by writers on the controversy.

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<sup>2</sup> Smithsonian Reports: 1914, pp. 9, 219, 221, 222; 1915, pp. 14, 121; 1917, p. 4; 1918, pp. 3, 28, 114, 166. Report of U. S. National Museum, 1914, pp. 46 and 47.

In January 1942, Mr. Fred C. Kelly, of Peninsula, Ohio, communicated to me a list of differences between the Langley plane as tested in 1914 and as tested in 1903, which he had received from Dr. Wright. This list is given verbatim below. The Institution accepts Dr. Wright's statement as correct in point of facts. Inferences from the comparisons are primarily the province of interested experts and are not discussed here.

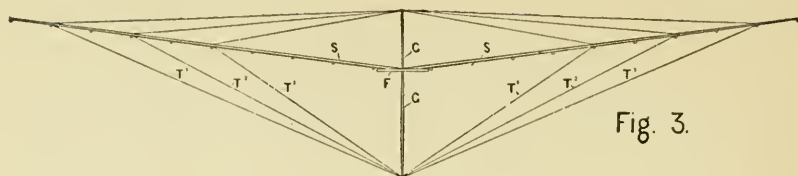
# COMPARISON OF THE LANGLEY MACHINE OF 1903 WITH THE HAMMONDSPORT MACHINE OF MAY-JUNE, 1914.

## LANGLEY, 1903.

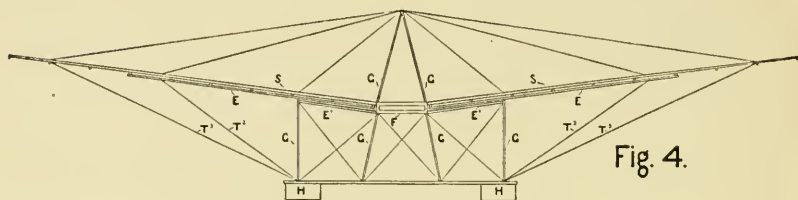
## HAMMONDSPORT, 1914.

### WINGS.

- |   |  |
|---|--|
| 1 SIZE: 11'6" x 22'6" (L.M. p. 206)   | SIZE: 10'11 $\frac{3}{4}$ " x 22'6"  |
| 2 AREA: 1040 sq. ft. (L.M. p. 206)  | AREA: 988 sq. ft.  |
| 3 ASPECT RATIO: 1.96  | ASPECT RATIO: 2.05   |
| 4 CAMBER: 1/12 (L.M. p. 205)  | CAMBER: 1/18   |
| 5 LEADING EDGE: Wire 1/16" diameter (L.M. Pl.66)  | LEADING EDGE: Cylindrical spar 1 $\frac{1}{2}$ " dia. at inner end, tapering to 1" dia. at outer end.  |
| 6 COVERING: Cotton fabric, not varnished.   | COVERING: Cotton fabric, varnished.  |
| 7 CENTER SPAR: Cylindrical wooden spar, measuring 1 $\frac{1}{2}$ " dia. for half its length and tapering to 1" at its tip. (L.M. p. 204). Located on upper side of wing. | CENTER SPAR: Cylindrical spar about 1 $\frac{1}{2}$ " dia. at inner end, tapering to about 1" dia. at outer end. Located on upper side of wing. This center spar was reinforced (1) by an extra wooden member on the under side of the wing, which measured 1" x 1 $\frac{1}{2}$ " and extended to the 7th rib from the center of the machine; and (2) by another wooden reinforcement on the under side extending out about one-fourth of the length of the wing. |
| 8 RIBS: Hollow box construction. (L. M. Plates 66,67)   | RIBS: Most of the original Langley box ribs were replaced with others made at Hammondsport. (Manly letter, 1914). The Hammondsport ribs were of solid construction and made of laminated wood. That part of the rib in front of the forward spar was entirely omitted.   |



LANCLEY WING TRUSSING 1903.



HAMMONDSPORT WING TRUSSING 1914.

- 9 LOWER GUY-POSTS: A single round wooden post for each pair of wings (see Fig. 3),  $1\frac{1}{4}$ " in dia.  $6\frac{1}{2}$ ' long. (L.M. Plate 62, p. 184).
- 10 The front wing guy-post was located  $28\frac{1}{2}$ " in front of the main center spar. (L.M. Plate 53).
- 11 The rear wing guy-post was located  $31\frac{1}{2}$ " in front of the main center spar. (L.M. Plate 53).
- 12 UPPER GUY-POSTS: For each pair of wings a single steel tube  $\frac{3}{4}$ " dia., 43" long. (L.M. p. 184, pl. 62).
- 13 Front wing upper guy-post located  $28\frac{1}{2}$ " in front of the main center spar. (L.M. pl. 53).
- 14 The rear wing upper guy-post was located  $31\frac{1}{2}$ " in front of the main center spar. (L.M. pl. 53).
- 15 TRUSSING: The wing trussing wires were attached to the spars at the 5th, 7th and 9th ribs out from the center (L.M. pl. 54). The angles between these wires
- LOWER GUY-POSTS: Four for each pair of wings (see Fig. 4), two of which were of streamline form measuring  $1\frac{1}{4} \times 3\frac{1}{2} \times 54$ " long; and two measuring  $2 \times 2$ " with rounded corners,  $3'9$ " long.
- The front wing guy-posts were located directly underneath the main center spar,  $28\frac{1}{2}$ " further rearward than in 1903.
- The rear wing guy-posts were located directly under the main center spar,  $31\frac{1}{2}$ " further rearward than in 1903.
- UPPER GUY-POSTS: For each pair of wings, two streamline wooden posts each  $1\frac{1}{4} \times 3\frac{1}{2}$ ", 76" long, forming an inverted V. (See Fig. 4).
- Front wing upper guy-posts located directly over main spar,  $28\frac{1}{2}$ " further rearward than in 1903.
- The rear wing guy-posts were located directly over the main center spar,  $31\frac{1}{2}$ " further rearward than in 1903.
- TRUSSING: A different system of wing trussing was used, and the wing trussing wires were attached to the spars at the 3rd, 6th and 9th ribs from the center. The angles between these wires

and the spars to which they were attached are shown in Fig. 3.

and the spars to which they were attached were all different from those in the original Langley machine. (See Fig. 4).

#### CONTROL SURFACES.

16 VANE RUDDER: A split vane composed of two surfaces united at their leading edges and separated 15" at their trailing edges, thus forming a wedge. Each surface measured 2'3" x 4'6", with aspect ratio .5. (L.M. p. 214, pls. 53,54).

VERTICAL RUDDER: The Langley vane rudder was replaced by a single plane vertical rudder which measured 3'6" x 5', with aspect ratio of .7.

17 Operated by means of a wheel located slightly in front of the pilot at his right side and at the height of his shoulder (L.M. p. 216, pls. 53,54).

Operated at Hammondsport through the Curtiss steering wheel in some tests, (Zahm affidavit pp. 5, 6), through the Curtiss shoulder yoke in some others (Manly letter, 1914), and fixed so as not to be operable at all in still others, (Zahm affidavit p. 7).

18 Used for steering only. (L.M. p. 214).

Used "as a vertical aileron to control the lateral poise of the machine", (Zahm affidavit p. 6) as well as for steering, (Zahm affidavit p. 7).

19 PENAUD TAIL: This was a dart-shaped tail having a vertical and a horizontal surface (Penaud tail), each measuring 95 sq. ft. It was located in the rear of the main frame.

TAIL RUDDER: Same size and construction as in 1903.

20 Attached to a bracket extending below the main frame.

Attached to same bracket at a point about 8" higher than in 1903.

21 "Normally inactive", (L. M. p. 216) but adjustable about a transverse horizontal axis by means of a self-locking wheel located at the right side of the pilot, even with his back, and at the height of his shoulder. (L.M. pls. 51, 53).

Operable about a transverse horizontal axis and connected to a regular Curtiss elevator control post directly in front of the pilot (Zahm affidavit p. 5).

22 Immovable about a vertical axis. (L.M. p. 214, pl.56, Fig. 1). No means were provided for adjusting this rudder about a vertical axis in flight. "Although it was

Immovable about a vertical axis on May 28, 1914, only. Thereafter it was made movable about a vertical axis and was connected through cables to a Curtiss steering wheel mounted on a

necessary that the large aerodrome should be capable of being steered in a horizontal direction, it was felt to be unwise to give the Penaud tail and rudder motion in the horizontal plane in order to attain this end". (L.M. p. 214).

- 23 KEEL: A fixed vertical surface underneath the main frame measuring 3'2" in height by 6' average length. Area 19 sq. ft. (L.M. pl. 53).

Curtiss control post directly in front of the pilot.

KEEL: Entirely omitted.

#### SYSTEM OF CONTROL.

- 24 LATERAL STABILITY: The dihedral only was used for maintaining lateral balance. (L.M. p. 45).

LATERAL STABILITY: Three means were used for securing lateral balance at Hammondsport: The dihedral angle as used by Langley, a rudder which "serves as a vertical aileron" (Zahm affidavit p. 6), and the Penaud tail rudder. The last two constituted a system "identical in principle with that of Complainant's [Wright] combined warping of the wings and the use of the vertical rudder". (Zahm affidavit p. 6).

- 25 LONGITUDINAL STABILITY: Langley relied upon the Penaud system of inherent stability for maintaining the longitudinal equilibrium. "For the preservation of the equilibrium [longitudinal] of the aerodrome, though the aviator might assist by such slight movements as he was able to make in the limited space of the aviator's car, the main reliance was upon the Penaud tail." (L.M. p. 215).

LONGITUDINAL STABILITY: At Hammondsport the Penaud inherent longitudinal stability was supplemented with an elevator system of control.

- 26 STEERING: Steering in the horizontal plane was done entirely by the split-vane steering rudder located underneath the main frame. (L.M. p. 214).

STEERING: On one day, May 28, 1914, steering in the horizontal plane was done with the vertical rudder which had been substituted for the original Langley split-vane steering rudder. After May 28th the steering was done by the vertical surface of the tail rudder (Zahm affidavit p. 7), which in 1903 was immovable about a vertical axis, (L.M. p. 214).



## POWER PLANT.

- |    |   |   |
|----|---|---|
| 27 | MOTOR: Langley 5 cylinder radial.   | MOTOR: Langley motor modified.  |
| 28 | IGNITION: Jump spark with dry cell batteries. (L.M. p. 262).  | IGNITION: Jump spark with magneto.  |
| 29 | CARBURETOR: Balzer carburetor consisting of a chamber filled with lumps of porous cellular wood saturated with gasoline. The air was drawn through this wood. There was no float feed. (L.M. p. 225). | CARBURETOR: Automobile type with float feed.                                    |
| 30 | RADIATOR: Tubes with radiating fins.  | RADIATOR: Automobile radiator of honeycomb type.                                |
| 31 | PROPELLERS: Langley propellers (L.M. pl.53, pp. 178-182).   | PROPELLERS: Langley propellers modified "after fashion of early Wright blades". |

## LAUNCHING AND FLOATS.

- |    |   |  |
|----|---|--|
| 32 | LAUNCHING: Catapult mounted on a houseboat.   | LAUNCHING: Hydroplanes, developed 1909-1914, attached to the machine.  |
| 33 | FLOATS: Five cylindrical tin floats, with conical ends, attached to underside of main frame at appropriate points, and about six feet above lowest part of machine. | FLOATS: Two wooden hydroplane floats, mounted beneath and about 6 feet to either side of the center of the machine at the lateral extremities of the Pratt system of trussing used for bracing the wing spars of the forward wings; and one (part of the time two) tin cylindrical floats with conical ends, similar to but larger than the Langley floats, mounted at the center of the Pratt system of trussing used for bracing the rear wings. All of the floats were mounted from four to five feet lower than the floats of the original Langley, thus keeping the entire machine above the water. |

## WEIGHT.

- |    |  |  |
|----|--|--|
| 34 | TOTAL WEIGHT: With pilot 850 pounds (L.M. p. 256). | TOTAL WEIGHT: With pilot, 1170 pounds.               |
| 35 | CENTER GRAVITY: 3/8" above line of thrust.         | CENTER GRAVITY: About one foot below line of thrust. |

Since I became Secretary, in 1928, I have made many efforts to compose the Smithsonian-Wright controversy, which I inherited. I will now, speaking for the Smithsonian Institution, make the following statement in an attempt to correct as far as now possible acts and assertions of former Smithsonian officials that may have been misleading or are held to be detrimental to the Wrights.

1. I sincerely regret that the Institution employed to make the tests of 1914 an agent who had been an unsuccessful defendant in patent litigation brought against him by the Wrights.

2. I sincerely regret that statements were repeatedly made by officers of the Institution that the Langley machine was flown in 1914 "with certain changes of the machine necessary to use pontoons", without mentioning the other changes included in Dr. Wright's list.

3. I point out that Assistant Secretary Rathbun was misinformed when he stated that the Langley machine "without modification" made "successful flights".

4. I sincerely regret the public statement by officers of the Institution that "The tests" [of 1914] showed "that the late Secretary Langley had succeeded in building the first aeroplane capable of sustained free flight with a man."

5. Leaving to experts to formulate the conclusions arising from the 1914 tests as a whole, in view of all the facts, I repeat in substance, but with amendments, what I have already published in Smithsonian Scientific Series, Vol. 12, 1932, page 227:

The flights of the Langley aerodrome at Hammondsport in 1914, having been made long after flying had become a common art, and with changes of the machine indicated by Dr. Wright's comparison as given above, did not warrant the statements published by the Smithsonian Institution that these tests proved that the large Langley machine of 1903 was capable of sustained flight carrying a man.

6. If the publication of this paper should clear the way for Dr. Wright to bring back to America the Kitty Hawk machine to which all the world awards first place, it will be a source of profound and enduring gratification to his countrymen everywhere. Should he decide to deposit the plane in the United States National Museum, it would be given the highest place of honor, which is its due.











SMITHSONIAN MISCELLANEOUS COLLECTIONS

VOLUME 103, NUMBER 9

MYSTACOCARIDA, A NEW ORDER OF  
CRUSTACEA FROM INTERTIDAL  
BEACHES IN MASSACHUSETTS  
AND CONNECTICUT

(WITH TWO PLATES)

BY

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Biology Department, University  
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# MYSTACOCARIDA, A NEW ORDER OF CRUSTACEA FROM INTERTIDAL BEACHES IN MASSACHU- SETTS AND CONNECTICUT

By ROBERT W. PENNAK

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AND

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(WITH 2 PLATES)

During the course of recent investigations on the ecology of the micrometazoa inhabiting the capillary waters of intertidal beaches in Massachusetts and Connecticut (Pennak, 1942a, 1942b; Zinn, 1942), more than 65 specimens of a small peculiar entomostracan were found. When these organisms were first examined superficially it was thought that they were copepods. In size, in their basic 16-segmented structure, in the general organization of the body into head, thorax, and abdomen, and in the number and arrangement of the appendages (see pl. 1, fig. 3), they appeared to be an aberrant species of Harpacticoida. A more detailed study, however, revealed that in certain fundamental anatomical features they were markedly different from copepods—so different, in fact, as to warrant the erection of a new order, the order Mystacocarida. A brief diagnosis of this group is given in the following paragraph.

## ORDER MYSTACOCARIDA

The Mystacocarida are microscopic Entomostraca inhabiting the interstitial waters of intertidal beaches. Only females are known. The body is colorless, distinctly segmented, cylindrical, vermiform, and elongate; it is divided into a large head, a single-segmented post-cephalosome, a 4-segmented thorax, and a 6-segmented abdomen. The head is elongate, with a cephalic shield, prominent rostrum, and ocelli; it bears two pairs of antennae, a labrum, a pair of mandibles, and two pairs of maxillae. The first antennae are large, elongate, uniramous, and sensory. The second antennae are prominent, biramous, sensory, and elongate. The large labrum is flat, broad, and movable; it is at-

tached to the head between the bases of the antennae and extends posteriorly as far as the postcephalosome. The mandibles are biramous and unmodified, while the first and second maxillae are uniramous and elongate. The postcephalosome bears a pair of flat, broad, irregular mouthparts (ordinarily corresponding to the maxillipeds of other groups). Each thoracic segment has a pair of small, unsegmented lamellar appendages. The terminal (anal) segment bears two large caudal rami which have prominent setae. None of the appendages are prehensile. The dense setation of the median margins of the mouthparts indicates that the *Mystacocarida* probably feed by straining particles of food from the interstitial water. They move through the capillary spaces by wormlike wriggling movements aided by natatory movements of the second antennae, mandibles, and to some extent the first and second maxillae. Most of the body segments are provided with a pair of lateral, dorsoventral, shallow troughs which have heavily chitinized edges. The indistinct genital aperture is on the first thoracic segment, and the anus is on the last abdominal segment between the bases of the caudal rami. Several larval stages have been found. Only one species is known.

So far as is known, the *Mystacocarida* are confined to the intertidal zones of marine beaches. They are a part of the complex community of bacteria, protozoa, and microscopic metazoa including harpacticoid copepods, Tardigrada, Nematoda, Oligochaeta, Acarina, and several other groups which inhabit the capillary water between the grains of sand. The *Mystacocarida* are probably facultative anaerobes since they may occur in portions of the intertidal sand where oxygen may be either absent or present in small quantities.

Superficially, the Copepoda and the *Mystacocarida* are somewhat similar. The two groups may be most easily distinguished from each other, however, on the basis of the number of segments comprising the head, thorax, and abdomen. In copepods the maxilliped segment is fused with five other anterior segments to form the head, and, in addition, the first thoracic segment is usually fused with the head, the whole thus constituting a cephalothorax. In the *Mystacocarida*, on the other hand, both the maxilliped segment and the first thoracic segment are distinct and separate from the head. Furthermore, the maxilliped segment is clearly separated from the thorax by a ventral constriction. According to the terminology of Sars (1901, 1903-1911) as clarified by Monk (1941), copepods typically have five thoracic (metasome) segments and five abdominal (urosome) segments. Although there are 10 segments posterior to the maxilliped segment in the *Mystacocarida*, there is no specialized movable articulation between

thorax and abdomen. The first four segments following the maxilliped segment, however, bear appendages which presumably are comparable with the thoracic appendages of the Copepoda. There are no signs or rudiments of a pair of appendages which would indicate the fifth thoracic segment. The maxilliped segment is so distinctive and unique, and is so sharply set off from the adjacent regions of the body in the Mystacocarida, that it may be conveniently termed a postcephalosome. The body of the Mystacocarida therefore may be divided into a head, a single-segmented postcephalosome, a 4-segmented thorax, and a 6-segmented abdomen.

Except for the first and second antennae, the appendages of the Mystacocarida differ markedly from those of the Copepoda (see pls. 1 and 2). The mandibles are biramous and elongate, the first and second maxillae are uniramous and elongate, and the postcephalosome appendages (maxillipeds) are irregular, broad, and flat. The large size and the dense median setation of the relatively unspecialized and primitive mouthparts indicate that they function in straining food particles out of the interstitial water of sandy beaches. The smaller mouthparts of the Copepoda, on the other hand, are usually composed of relatively few segments and are more or less specialized for the manipulation of food; this is especially true of harpacticoid copepods which inhabit sandy beaches. Not only are the trophic rami of the Mystacocarida large and unspecialized, but also the head is proportionately much longer than it is in the Copepoda. All of the thoracic appendages show a reduction and simplicity found only in the fifth legs of a few copepods. Each leg is a simple, unsegmented lamella which is probably useless in swimming or crawling.

Between the bases of the mouthparts of the Mystacocarida there is an enormous, movable, broad, flat labrum. The labrum of the Copepoda is an insignificant structure.

On the posterior part of the cephalic shield, on the maxilliped segment, on each thoracic segment, and on each of the first five abdominal segments, there is a pair of lateral, dorsoventral, shallow troughs with heavily chitinized, sculptured edges. Structures of a somewhat similar nature are known in only one species of Copepoda (Zinn, 1942). No function can be ascribed to them.

Finally, the Mystacocarida may be differentiated from the Copepoda on the basis of the location of the genital pore; in the former group it is on the first thoracic segment, while in the latter it is on the last thoracic segment.

The peculiar location of the genital pore in the Mystacocarida represents an unusual condition. In the great majority of Crustacea the genital pore is at or near the posterior end of the thorax. Indeed, according to the Calman scheme, the thorax is defined as that region behind the head and in front of, and including, the segment which bears the male genital pore; also, with the exception of the hermaphroditic Cirripedia, the female genital pore is on the last or third-last thoracic segment. Such a definition is arbitrary, to be sure, but it is in striking contrast to the situation in the Mystacocarida.

In spite of the numerous significant morphological differences between the Copepoda and the Mystacocarida, the similar segmentation, the general body organization, and the number and arrangement of the appendages constitute convincing evidence that these two orders are very closely related. Certainly it does not seem possible to demonstrate important phylogenetic affinities between the Mystacocarida and any other order.

Undoubtedly, the Mystacocarida are the most primitive living Crustacea which have thus far been discovered. In addition to the simple body organization, this is clearly indicated by the persistence of larval characters in the head, including the unspecialized primitive morphology of the large mouthparts, the labrum, and the rostral shield. The lamellar structure of the abdominal appendages, on the other hand, is obviously a reduced condition.

#### DEROCHEILOCARIDAE, new family

Characters as of the type genus, *Derocheilocaris*

#### DEROCHEILOCARIS, new genus

Body elongate and cylindrical; all segments clearly marked off from each other; thorax and abdomen about the same diameter throughout; head and postcephalosome distinctly narrower than rest of body. Head covered with a cephalic shield which has a large rostral plate bearing a prominent, notched rostrum. Anal segment with a large papilla dorsal to the anus. A pair of lateral, dorsoventral troughs with heavily chitinized edges on the posterior part of the cephalic shield and on all other segments except the last.

First antennae 8-segmented, the terminal segment longest. Second antennae tactile and natatory; both rami elongate. Both rami of mandibles elongate, but endopod distinctly shorter than exopod; gnathobase on basipod. Instead of projecting ventrally, the second antennae and mandibles are flexed so that they extend dorsally and laterally away from the median plane of the body. Labrum very

large and flat; posterior end, between bases of maxillipeds, forming a broad, smooth semicircle at its extremity. First maxillae uniramous, elongate, and composed of seven segments. Second maxillae uniramous, elongate, and 6-segmented; segments not so broad as those of first maxillae. Postcephalosome appendages (maxillipeds) irregular, flat, and broad; not distinctly divisible into exopod and endopod. Each thoracic appendage reduced to a small, simple, unsegmented lamella bearing a few terminal setae. Each caudal ramus prominent and curved dorsally to form a large terminal claw.

*Genotype*.—*Derocheilocaris typicus*.

DEROCHEILOCARIS TYPICUS, new species

PLATES I AND 2

Head about one-third as long as the rest of the body and separated from postcephalosome by a ventral constriction. Head and postcephalosome distinctly narrower than rest of body. Thoracic and abdominal segments all about the same size. Rostral plate separated from cephalic shield by a well-defined groove, and with three prominent notches at its anterior edge. The median notch is deep and ovoid. The lateroventral notches are also deep but are more nearly circular and are toothed along the ventral margins; it is possible that these may be remnants of chitinous troughs. Near the posterior margin of the median notch are several eyespots. Their number and exact position are variable but typically there are two pairs, one of which is rather small and close to the median line at the posterior end of the notch, while the other two ocelli are larger and more anterior and lateral. The last segment has a prominent median dorsal papilla which bears a single seta and a minute toothed papillule. On each side of the dorsal papilla there is a broadly triangular, flat, short, spinous process. The two caudal rami are slightly longer than the last segment, broad at the base, and are curved dorsally in the form of a large claw. Each ramus bears three large plumose setae, one dorsal and two lateral. The two lateral setae originate at about midlength of the ramus, one being slightly shorter than the ramus and the other about twice as long as the ramus. The dorsal seta originates near the base of the ramus and is slightly longer than the ramus. There are two small papillae on the dorsal surface of each ramus, the anterior one bearing a fine seta. Along the median ventral edge of each ramus are three small equidistant processes each of which bears a spinule.

The lateral chitinous troughs of the head are situated near the posterior margin of the cephalic shield; each of these is roughly



elongate but the dorsal and ventral extremities are irregular in outline; there are six to eight minute chitinous teeth along both the anterior and posterior edges. The troughs of the postcephalosome are irregular in shape but roughly cross-shaped with the vertical axis longer than the horizontal axis; there are four groups of one to four teeth along the inner margin of these two troughs. The troughs of the thorax and abdomen are situated in approximately the middle of the segments. They are all similar, being long and narrow with 10 to 14 triangular interlocking teeth on each side.

The location of the genital pore on the ventral side of the first thoracic segment is indistinctly indicated by the presence of a broadly obtuse chitinous ridge which projects anteriorly and ventrally near the anterior margin of the segment.

The first antennae are long and 8-segmented; the first three segments are short and broad, but the others are elongate, the terminal segment being the longest. The first segment bears one seta; the second has three, two of which are minute; the third has seven, four of which are minute; the fourth through eighth segments bear 3, 4, 4, 5, and 3 to 5 terminal setae, respectively. The first and second segments each have a small dorsal hook, and the terminal segment bears a single delicate aesthetask.

The second antennae are biramous with the 5-segmented endopod being about half again as long as the 9-segmented exopod. The basal endopod segment bears two short median setae while the third segment has a single seta. The terminal endopod segment is long and fingerlike and bears a fringe of fine hairs at its tip. The exopod segments are short; segments one, four, five, and six have a single short seta, while the seventh and eighth have a long plumose seta; the terminal segment is tipped with three long plumose setae. There are five aesthetasks, one on the basipod, one on the first exopod segment, one on the third, and two on the terminal segment. All the aesthetasks project laterally. Because of their delicacy they are often broken off in specimens which have been permanently mounted on slides.

The mandibles are of a generalized larval type. The 2-segmented endopod is about two-thirds as long as the 7-segmented exopod. The basal endopod segment bears a single median seta, while the other has two median and three terminal setae. Exopod segments three, four, five, and six bear a single terminal seta, the last three of which are plumose. The last exopod segment has three terminal plumose setae, two of which are short while the third is slightly more than twice the length of the entire exopod. The basipod bears a single

distal median seta and a prominent, curved, stout, spinelike gnathobase which has several small median spinules. All the segments of the mandibles are beset with small rows of fine hairs.

The seven segments of the uniramous first maxillae are somewhat broad and flat, the third segment being the largest. The basal segment is narrowed at its base where it is attached to the trunk; the second segment is short and is set off from the first and third segments by poorly defined articulations. Except for one small lateral seta on the sixth segment, all of the setae are stout and are arranged along the median margins of the segments (median and terminal margins in the case of the last segment). Beginning with the basal segment the setation of the first maxillae is 3-1-4-2-2-2-8. All of the setae except those of the terminal segment are borne on small projections.

The uniramous 6-segmented second maxillae are narrower and slightly longer than the first maxillae. The first and second segments are considerably larger than the other four. Like the first maxillae, these appendages are densely setose along the median margins; typically, the setation is 8-8-2-2-2-5. Three of the setae of the basal segment are borne on a prominent process; two setae of the terminal segment and one on the fifth segment are geniculate.

The structure of the postcephalosome appendages (maxillipeds) is unique. They are small, irregular, but somewhat elongate, and usually lie appressed to the trunk. It is likely that several exopod and endopod segments have become fused with the basipod to form the main body of the maxilliped. The remnant of the exopod consists of three small segments, the second and third of which bear two setae. The remaining endopod segments comprise a small bilobed outgrowth which bears five setae. The large basal portion of this appendage has three small lateral and two small median processes all of which bear one or two broad setae.

In studying the first antennae, first maxillae, second maxillae, and maxillipeds of about 20 specimens, it was found that there are occasional variations in the number and precise positions of the setae.

The four pairs of thoracic appendages are small, simple, unsegmented lamellae which lie rather closely appressed to the trunk. They are all about the same size and differ only slightly in shape. The first, second, and fourth appendages are roughly oblong, while the third is tapered slightly, is more ovate, and has a small median notch at about half length. The first abdominal appendages have two terminal setae, while the others have three terminal setae.

From the tip of the rostrum to the posterior end of the caudal rami the length of the adult ranged from 409 to 491 microns; the average length was 458 microns.

Cotypes, U.S.N.M. No. 80450 from Nobska Beach, Mass., have been deposited in the United States National Museum.

*Larval stages.*—A few specimens of five different larval stages were found. For convenience in making comparisons, these larvae have been arbitrarily numbered 1, 2, 3, 4, and 5 in order of their increasing size, complexity, and maturity. All have two pairs of antennae, mandibles, labrum, second maxillae, and caudal rami. Only the two largest stages have first maxillae and maxillipeds, although all five stages have a maxilliped segment (postcephalosome).

Except for the second antennae and mandibles, all of the larval appendages are strikingly similar to the corresponding appendages of the adult. Attached to the basipod of the second antenna, and more median than the base of the endopod, is an unsegmented biramous quasi palp in all larval stages. The undivided basal portion of this quasi palp is very short while the two rami are about as long as the adjacent endopod (see pl. 2, fig. 8). The distal half of the outer ramus and the distal third of the inner ramus consist of two setae of similar length. In addition, the outer ramus has two small setae near its base. Also, the endopod of the larval second antenna has four segments while that of the adult has five.

The presence of the unique quasi palp on the larval second antennae suggests interesting conjectures. Although the quasi palp is not a very well-developed or robust structure, it is possible that it may function, or at one time did function, as a clasping organ. The possibility then arises as to whether the fifth larval stage may be (or may have been in the past) a functional male phase as is the case in certain other protandrous Crustacea, Mollusca, and Nematoda. In none of the fifth larval stages, however, could any internal reproductive structures be discerned.

The endopod of the larval mandible also differs markedly from that of the adult. In the former it is composed of three broad segments, the terminal segment being much smaller than the other two. In the adult this ramus is composed of two long narrow segments.

The smallest larvae found have a total of only 3 segments posterior to the postcephalosome; the second smallest stage has 5 such segments; the next largest has 7; the other two have 10, the same as the adults. No thoracic appendages are present on the first three larval stages, but the fourth and fifth stages have 3 and 4 thoracic appendages, respectively. In all immature stages the posterior part of the cephalic shield, the postcephalosome, and all posterior segments except the last segment have chitinized troughs.

From the standpoint of morphological characteristics and size (see table 1), it is logical to assume that larval stage 4, larval stage 5, and the adult form a natural sequence. On the other hand, however, it seems very probable that the three earlier stages are an incomplete series and that there are still other early stages which were not discovered during the present investigation. It is particularly likely that there are very early larval stages which are comparable with copepod nauplii in their simplicity. Because of incomplete information concerning the various stages in the development of the Mystacocarida, therefore, no attempt will be made at this time to assign any descriptive, designative names to the five different types of larvae that are known.

TABLE 1.—*Summarized morphological characteristics of larval stages of Derocheilocaris typicus*

Larval stage	Number of segments in endopod of mandible	Quasi palp on basipod of mandibles	First maxillae	Postcephalosome segment	Maxillipeds	Number of thoracic and abdominal segments	Number of pairs of thoracic appendages	Average length, microns
1 .....	3	present	absent	present	absent	3	0	187
2 .....	3	present	absent	present	absent	5	0	203
3 .....	3	present	absent	present	absent	7	0	250
4 .....	3	present	present	present	present	10	3	350
5 .....	3	present	present	present	present	10	4	390
(adult)....	2	absent	present	present	present	10	4	458

*Internal anatomy.*—Although only a superficial study was made of the internal anatomy of *Derocheilocaris typicus*, it might be worth while to indicate a few of the more obvious structural details. In sexually mature individuals the most distinctive feature is a large, elongate, dorsal, granular yolk gland; the posterior end of this yolk gland extends as far as the fourth or fifth abdominal segment; anteriorly, it may not extend beyond the first abdominal segment, or it may extend as far forward as the second thoracic segment. The ovary consists of several immature ova (customarily three to seven); they are rather compactly arranged in the dorsal portion of the third and fourth thoracic segments; often the ovary is partially imbedded in the anterior portion of the yolk gland. A gonoduct could not be definitely distinguished. The digestive tract is tubular and without any pronounced constrictions or diverticula. Neither maxillary nor antennary glands could be discerned. The nervous system, as shown by longitudinal sections, is characterized by a series of extremely large

segmentally arranged ventral ganglia. There is considerably less fusion of the ganglia of the head than in other groups.

*Occurrence.*—Of five beaches examined in the vicinity of Woods Hole, Mass., *Derocheilocaris typicus* was found only in Nobska Beach near the town of Woods Hole and in a beach 5 km. east of Woods Hole near the town of Falmouth. About 50 mature and 12 immature specimens were collected during June and July, 1939. The great majority of these organisms occurred within a meter of the high-tide line at a depth of 12 to 16 cm. in the damp sand. Although many series of intertidal sand samples were collected at Baxter's Beach, Pine Orchard, Conn., between November 1937, and May 1942, this form was found only during April 1940.

#### ACKNOWLEDGMENTS

The senior author carried on the field work associated with this study during June and July, 1939, when he was a visiting investigator at the Woods Hole Oceanographic Institution. He wishes to express his gratitude to Prof. H. B. Bigelow, then director of the Institution, for his kindness in providing laboratory facilities. Both authors thank Prof. G. E. Hutchinson, of Yale University, for his many helpful suggestions.

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## EXPLANATION OF PLATES

## PLATE I

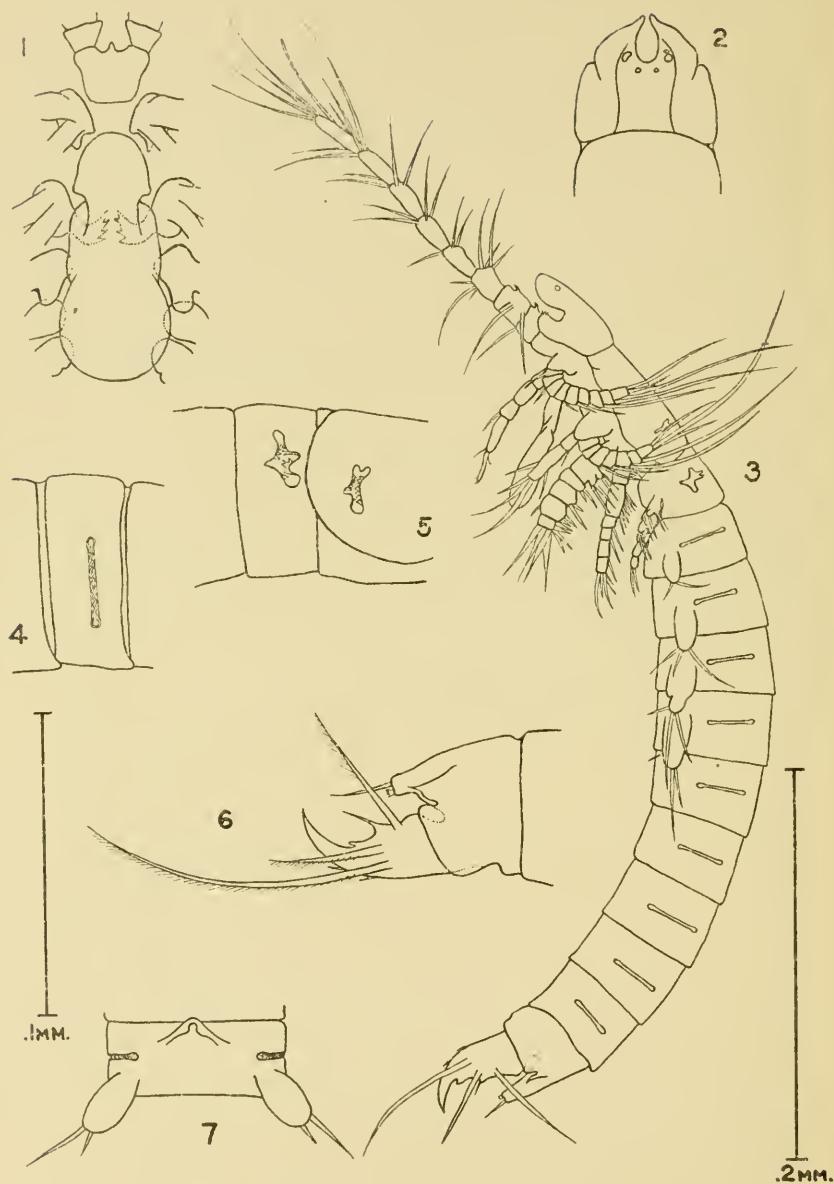
*Derocheilocaris typicus*

1. Ventral view of head region of adult showing relationships between labrum and basal portions of first antennae through maxillipeds.
2. Dorsal view of cephalic shield, showing notches, sutures, and ocelli.
3. Lateral view of adult.
4. Lateral view of abdominal segment showing detailed structure of a chitinous trough.
5. Lateral view of posterior part of head and postcephalosome showing details of chitinous troughs.
6. Lateral view of posterior end.
7. Ventral view of first thoracic segment showing region of genital opening. (Large scale refers to figure 3; small scale refers to all other figures.)

## PLATE 2

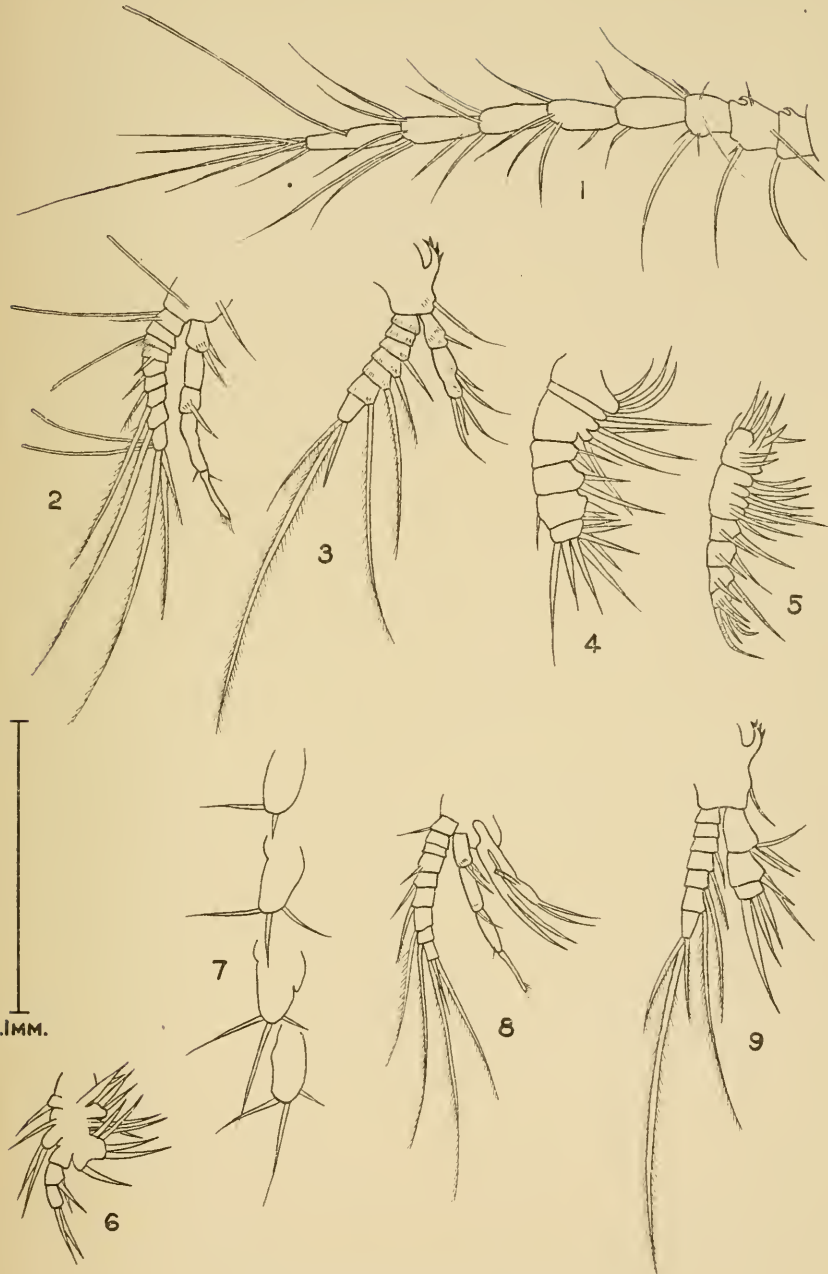
*Derocheilocaris typicus*

1. First antenna of adult.
2. Second antenna of adult.
3. Mandible of adult.
4. First maxilla of adult.
5. Second maxilla of adult.
6. Maxilliped of adult.
7. Right thoracic appendages of adult.
8. Second antenna of fifth larval stage.
9. Mandible of fifth larval stage.



**DEROCHEILOCARIS TYPICUS**

(For explanation, see page 11.)



**DEROCHEILOCARIS TYPICUS**

(For explanation, see page 11.)









SMITHSONIAN MISCELLANEOUS COLLECTIONS

VOLUME 103, NUMBER 10

(End of Volume)

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## Roebliug Fund

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# A REMARKABLE REVERSAL IN THE DISTRIBUTION OF STORM FREQUENCY IN THE UNITED STATES IN DOUBLE HALE SOLAR CYCLES, OF INTEREST IN LONG-RANGE FORECASTING

By C. J. KULLMER<sup>1</sup>

We have for the United States the only long fairly uniform series of maps of tracks of barometric depressions. These have been published in the Monthly Weather Review for each month from 1874 to the present. Dunwoody assembled the material for the 10-year international period, 1878-87, in storm-frequency maps for the whole Northern Hemisphere. Dunwoody's method was to divide the maps into 5° squares and record the number of centers of barometric depressions that crossed each square. In 1911 I remade the maps of storm frequency in the United States for 1899-1908 according to Dunwoody's plan of 5° squares.<sup>2</sup> In the interval of 21 years a slight but definite southerly and westerly shift had taken place. But 5° in latitude, about 345 miles, is evidently unnecessarily large if we wish to test latitude shifts. I wished to ascertain whether there is any correspondence between the latitude shifts of sunspots and the latitude of the vortexes in our own atmosphere. Accordingly, I cut Dunwoody's square in half, making the unit 5° in longitude and 2½° in latitude, and made in 1913 a series of year maps from 1874 to 1912, furnishing comparison material for three solar cycles. Since that time three more solar cycles have become available. The results for the five cycles, with a series of year maps, 1883-1930, appeared in 1933 in a Smithsonian publication.<sup>3</sup> I shall now present the results for the last solar cycle.

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<sup>1</sup> Published posthumously; Dr. Kullmer, formerly of Syracuse University, died in 1942.

<sup>2</sup> The shift of the storm track. Chap. 16 in Huntington, The climatic factor, Carnegie Inst. Publ. 192, 1914.

<sup>3</sup> Kullmer, C. J., The latitude shift of the storm track in the 11-year solar period, Smithsonian Misc. Coll., vol. 89, No. 2, 1933. Preliminary publication of parts of the study appeared in Huntington, The solar hypothesis of climatic changes, Bull. Geol. Soc. Amer., vol. 25, pp. 477-590, 1914. See also Huntington, Earth and Sun, Yale Univ. Press, 1923.

For comparison, the most powerful method of attack seemed to be to add together 3-year maps at solar minimum and 3-year maps at solar maximum and compare them with each other. This was done for five solar cycles, with the result that a uniform pattern appeared. In figure 1 I present one such cycle, perhaps the most typical of the five. Plus figures indicate the excess in years of solar maximum over years of solar minimum; minus figures, the reverse. In the north there was a strong increase along the main storm track, but also a southerly projection. I have drawn a heavy dotted line through the main area of excess at times of maximum and also through the projection; at both sides of the projection there are areas of decrease, i.e., more storms at years of minimum than at maximum. In figure 2 I have assembled the dotted lines through the area of excess and the projection. It will be noted that in the fifth period there was an unexpected move to the south and that the southerly projection had shifted even farther west than in the second period. Because of a certain orderly progression in the shifts of the southerly projection I ventured a hypothetical position for the sixth solar cycle, and was correct in assuming an easterly motion of the southerly projection. I now present in figure 3 the results for the last solar cycle, showing an unexpected still greater shift to the south of the main area of excess at solar maximum. There was some doubt as to the year of maximum, 1937 or 1938, and consequently I made the maps for both periods, figure 4. Except for slight variation in figures, the maps are identical.

Now what does the continued southerly shift of the pattern signify, with the large increases at minimum in western Canada? The interpretation of a relation between sunspot latitudes and latitudes of earthly storms seemed to be justified by the first four periods, but contradicted by the fifth and sixth periods. There remained one way to test the relationship. In figure 5, taken from Clayton's "World Weather," we have Maunder's chart of sunspot latitudes. All these years I have been comparing 3 years at solar minimum with 3 years at solar maximum, but evidently the latitude effect would be intensified if I compared 3 years at the beginning of the cycle with 3 years at the end of the cycle. There is a noticeable overlapping of the new cycle with the old; in order to avoid this source of error I would eliminate by inspection the year of maximum overlapping, as indicated in the chart, and proceed to test the latitude effect by comparing 3 years at the beginning of a cycle with 3 years at the end of a cycle. I began with the first cycle available, figure 6, and the results were a succession of surprises. Gone was all thought

of a relation to sunspot latitudes. Gone entirely was the pattern with the southerly projection, which I had found consistently for six solar cycles. This pattern still remains an enigma, the result of some solar relationship, the difference between years of maximum solar activity and those of minimum activity. Instead I discovered a solar relationship of possibly great significance.

The first period, figure 6, shows three horizontal bands. Plus figures indicate more storms at the beginning of the cycle; minus figures, more storms at the end of the cycle than at the beginning. The following period, figure 7, shows a map of an entirely different character—a plus band in the north, and curving down the Atlantic coast and across the south a minus area, forming a script T pattern. The succeeding period, figure 8, returns to the pattern of the first, three horizontal bands, but in reversed order, with a pronounced minus area between the plus bands. The succeeding map, figure 9, was the greatest surprise of all—a return to the almost identical script T pattern of the second period, but in reverse, with a minus area in the north and curving down the Atlantic coast, and across the south a plus area. And now with the fifth period, figure 10, we return to the three horizontal bands, but again in reverse, with a plus area between two still widened minus areas. These complicated relationships will appear more simple in a table, figure 11. Because of the appearance of three bands in the first and third period and the strange script T pattern in the second and fourth periods, we may divide the first four periods into two Hale solar cycles. But whatever the solar influence may be that determines the location of storms on earth, that influence was completely reversed in the two Hale cycles. The evidence of a reversal is further supported by the return in the fifth period to the conditions found in the first.

A crucial test will be offered by the coming sixth solar cycle, which will have to show the script T pattern with a plus area in the north and the long curved minus area in the south. Fortunately we are able to look somewhat into the future. I have combined the maps for 1935-1937, and they show the highest known figures for the eastern Canadian region. It might be considered that this shows merely the increase in the network of northern Canadian recording stations. But I present the evidence of the two squares in Quebec, north of the Gaspé. Figure 12 shows the number of barometric depressions that crossed these two squares from 1883 to 1940. This diagram is another evidence that tends to confirm my confidence in the early records of tracks of storms. The early years show approximately the same high frequency as the later years; the year 1894 with 56

barometric depressions almost equals the high of 1937 with 57 storms. We note that in 1895 there was a sudden drop from 56 to 17 and in a few years to 2. Furthermore, we notice that in 1940 there was a sudden drop from a high of 57 to 29 and that the interval between the two sudden drops was 45 years, exactly four solar cycles. I think there can be little question that the years of minimum, 1941-43, will show a decrease in eastern Canada. With the plus area in eastern Canada assured, we shall have to wait 3 or 4 years for the possible completion of the lower part of the script T pattern.

How shall we interpret these findings? We naturally first think of the alternations in solar activity as shown in the accompanying table, figure 13, and of Clayton's northerly shift of the centers of action with increased solar activity, but the figures resist attempts at correlation with the observed reversal. It seems, therefore, necessary to consider the theory that solar activity may possibly be completed in four cycles, of which the third and fourth are in some mysterious way the exact reversal of the first and second. We have become accustomed to the idea of a reversal of solar activity through Hale's discovery of a reversal of magnetic polarity with each new solar cycle. But in what way could such a Hale cycle itself be reversed?

Finally a word concerning the years selected for comparison. It will be remembered that for the first three and a half periods I selected by inspection from Maunder's chart of sunspot latitudes the years of maximum overlapping and used 3 years on either side of such a year. Maunder's chart does not include the minima of 1923 and 1933; consequently I selected these years as boundaries. Figure 14 summarizes the official years of minimum and maximum solar activity, together with my periods selected as described. I would call attention to the fact that the first and third periods begin 2 years after the official minimum; the second period, 1 year after minimum, and the fourth period begins with the minimum. There are very slight differences in the Wolfer sunspot numbers which determine the solar minimum, and it seemed worth while to test the matter by making a series of maps using the official minimum year as the boundary; for the fifth test period, which was originally so bounded, I included the minimum year and have already presented it as the superior map. In figure 15 I present the first period. The central plus band is strengthened, but the southern minus band is weakened. My original period seems to be the best for the three-banded effect. In the second period, figure 16, the plus band in the north is weakened, uncovering, as it were, a narrow band of minus which crosses the map. Also the southern curved minus area is

weakened. Again my original period is the best. In the third period, figure 17, the northern plus band is weakened; otherwise, there is little choice. The fourth period, figure 18, shows the greatest discrepancy, with a great weakening of the northern minus band and the introduction with the year 1916 of a new strong plus band. There is also a weakening of the southern plus curve. It is evident that for the solar influence presented in this paper my original period is far the superior. The last period, figure 19, shows a widening and strengthening of the northern minus band and I have consequently chosen it as the best representative of the three-banded effect. Why, with this one exception, my original periods best bring out the solar effect here presented I cannot venture an opinion; it is, however, of interest, that with the exception of the fourth period, a shift of 1 year, and in one case, of 2 years does not vitiate the results.

These, then, are my findings, and I offer them to those more competent than I am for interpretation.

I append the year maps of storm frequency for 1931-1940, forming a series of 58 year maps, made with care according to a uniform technique, to which can be added the years 1874-1882, now in manuscript.



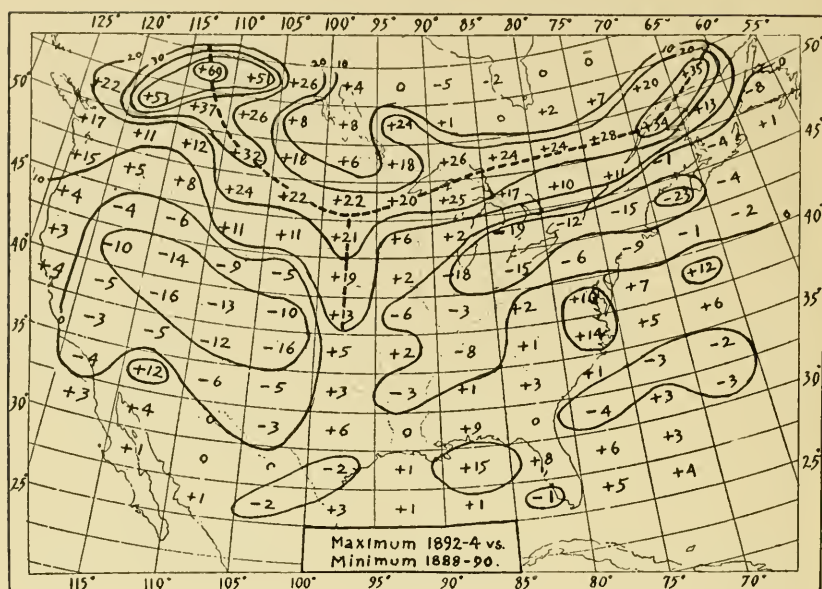


FIG. 1.

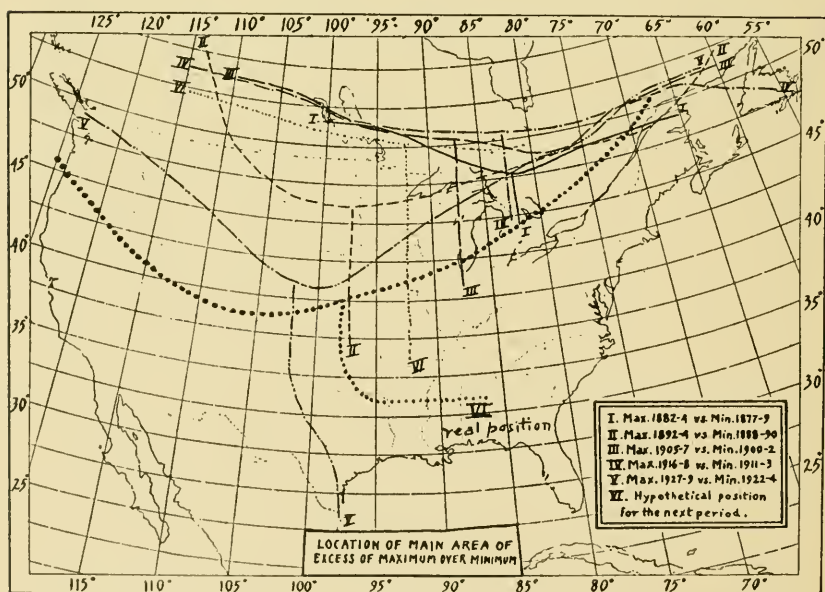


FIG. 2.

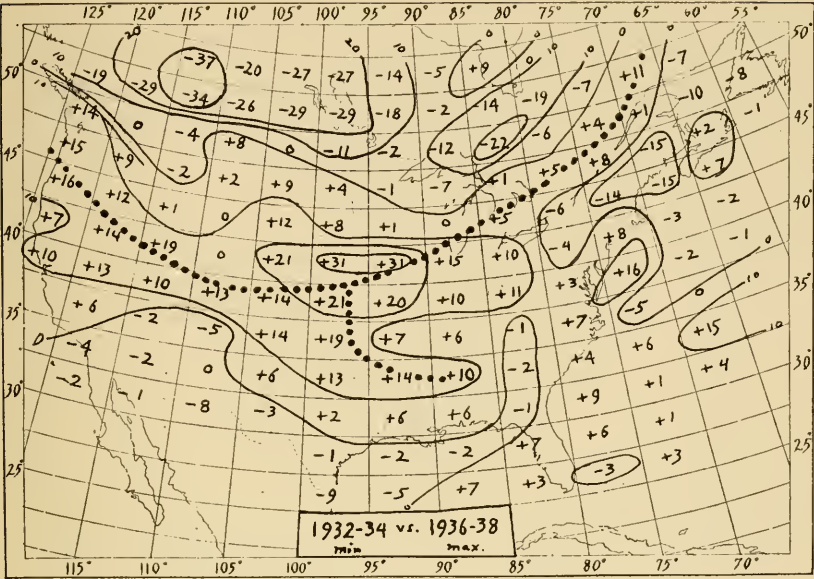


FIG. 3.

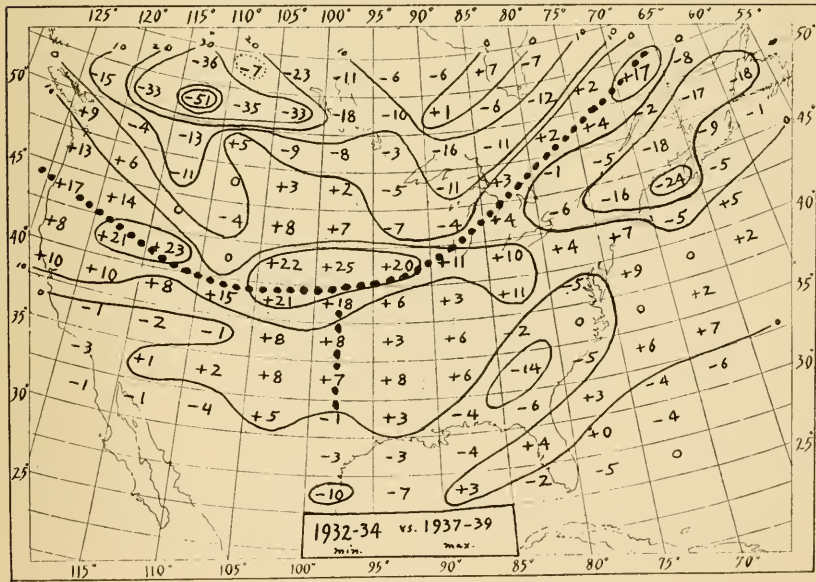


FIG. 4.

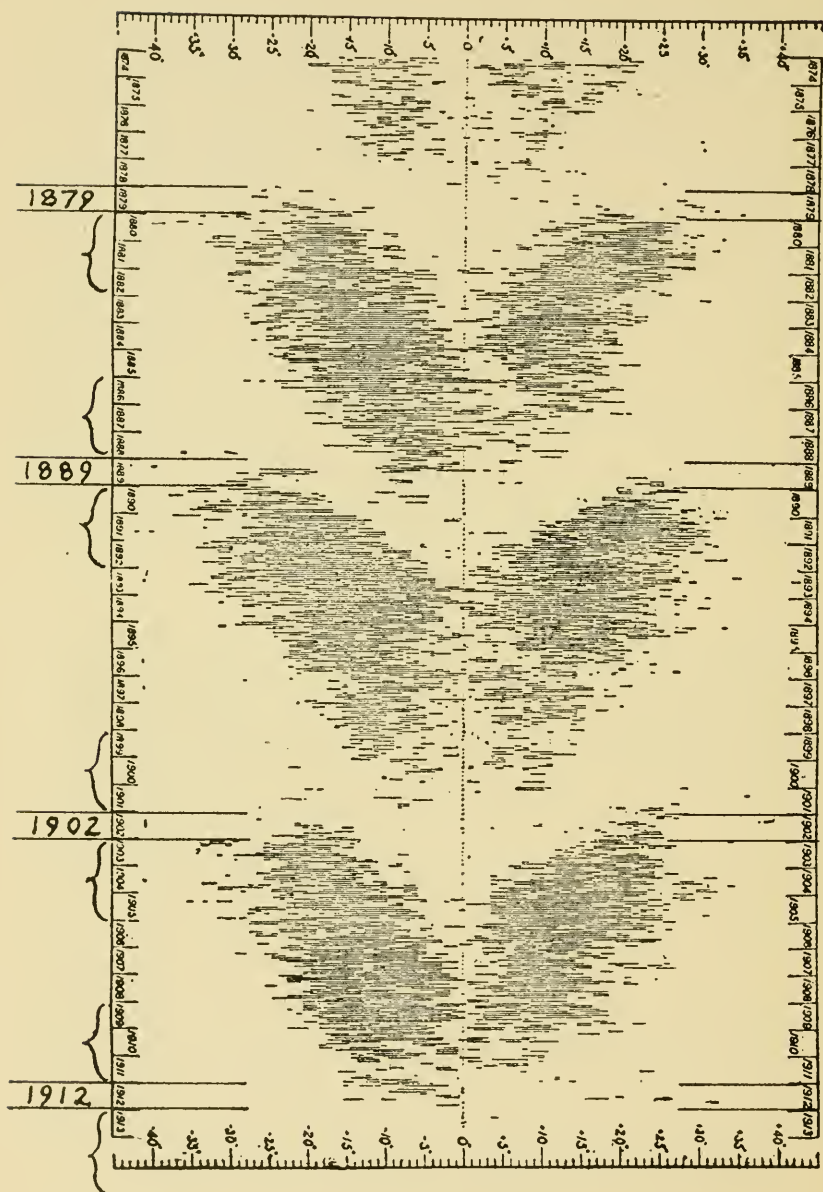


FIG. 5.

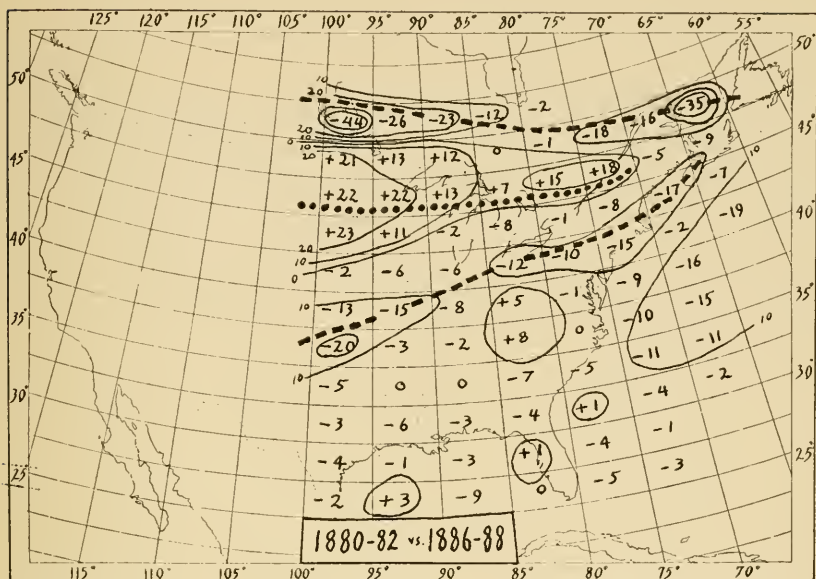


FIG. 6.

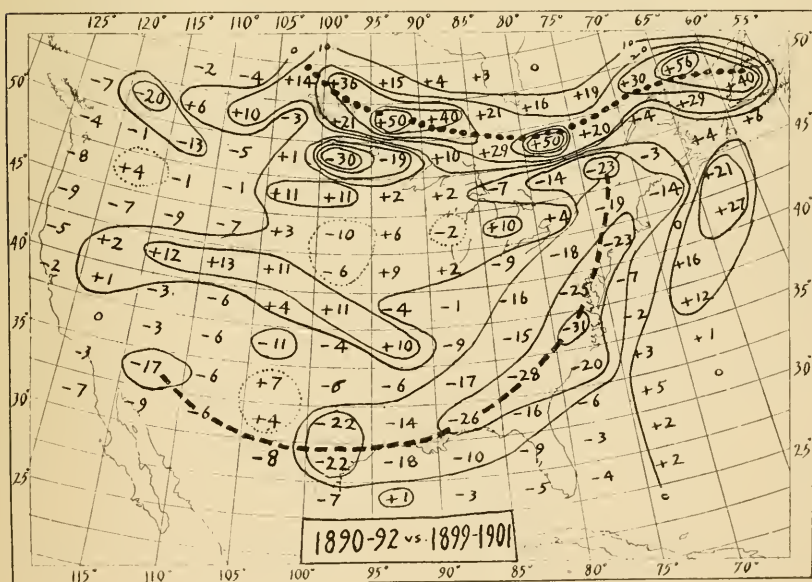


FIG. 7.



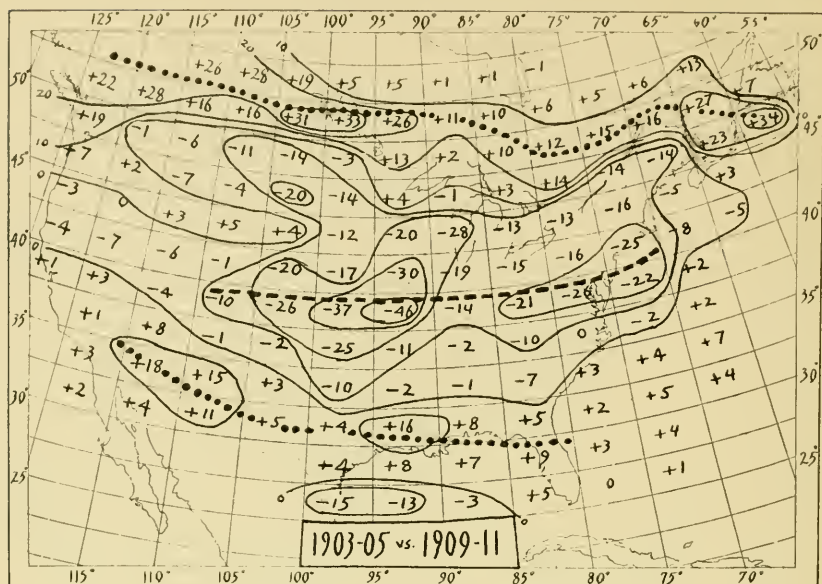


FIG. 8.

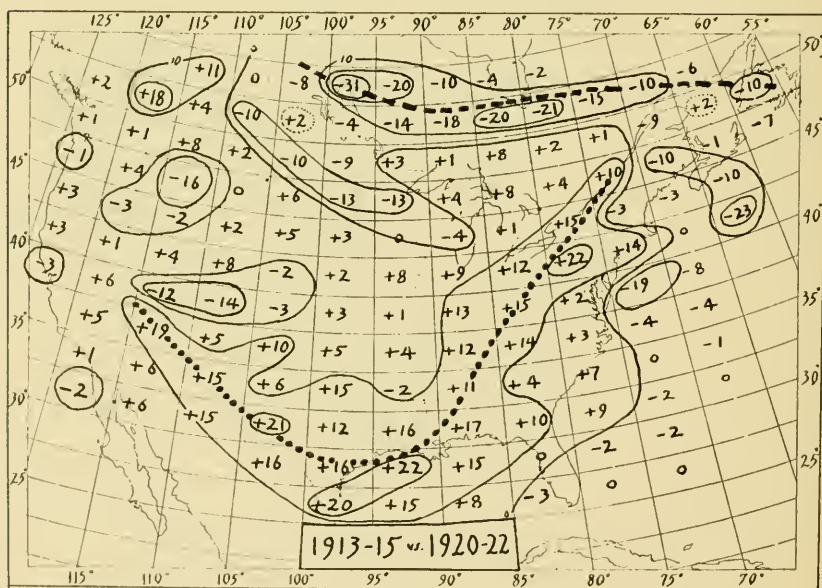


FIG. 9.



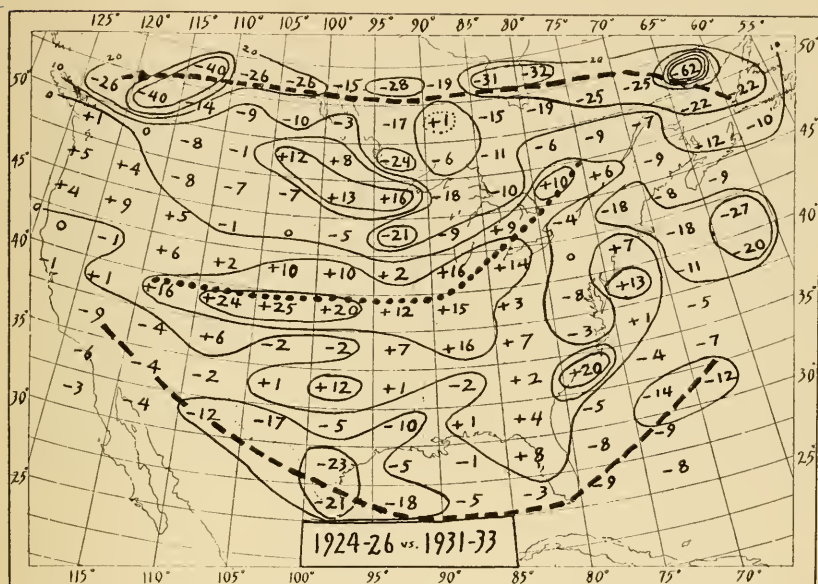


FIG. 10.

1880-82	1890-92	1903-05	1913-15	1924-26	1935-37
vs.	vs.	vs.	vs.	vs.	vs.
1886-88	1899-01	1909-11	1920-22	1931-33	1941-43?
Two bands		Two bands			
Three bands	in a	Three bands	in a	Three bands	?
	$\nabla$ pattern		$\nabla$ pattern		
minus	plus	plus	minus	minus	plus
plus	—	minus	—	plus	?
minus	minus	plus	plus	minus	

FIG. 11.

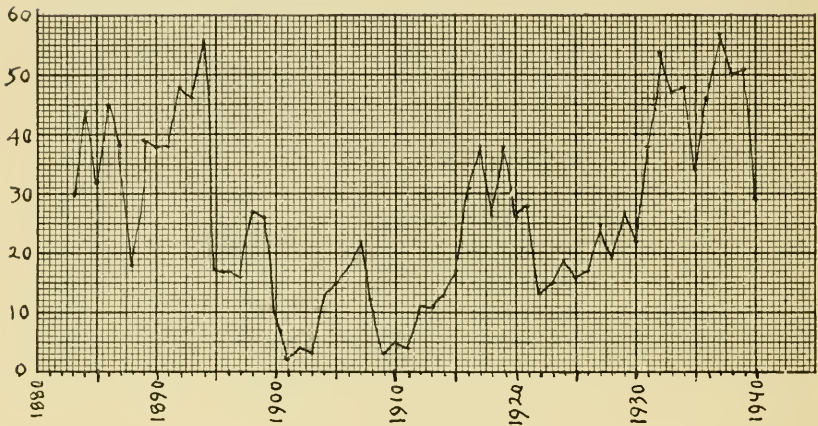


FIG. 12.

1870.....	Max.	139.1	
1883.....	Max.	63.7	Three Bands
1893.....	Max.	84.9	J Pattern
1905.....	Max.	63.5	Three Bands
1917.....	Max.	103.9	J Pattern
1928.....	Max.	77.8	Three Bands
1937.....	Max.	137.0	J Pattern

FIG. 13.

Years selected	Min.	Max.	Test years
1880-82 vs. 1886-88	1878	1883	1879-81 vs. 1886-88
1890-92 vs. 1899-01	1889	1893	1890-92 vs. 1898-00
1903-05 vs. 1909-11	1901	1905	1902-04 vs. 1910-12
1913-15 vs. 1920-22	1913	1917	1914-16 vs. 1920-22
1924-26 vs. 1930-32	1923	1928	1924-26 vs. 1931-33
	1933	1937	

FIG. 14.

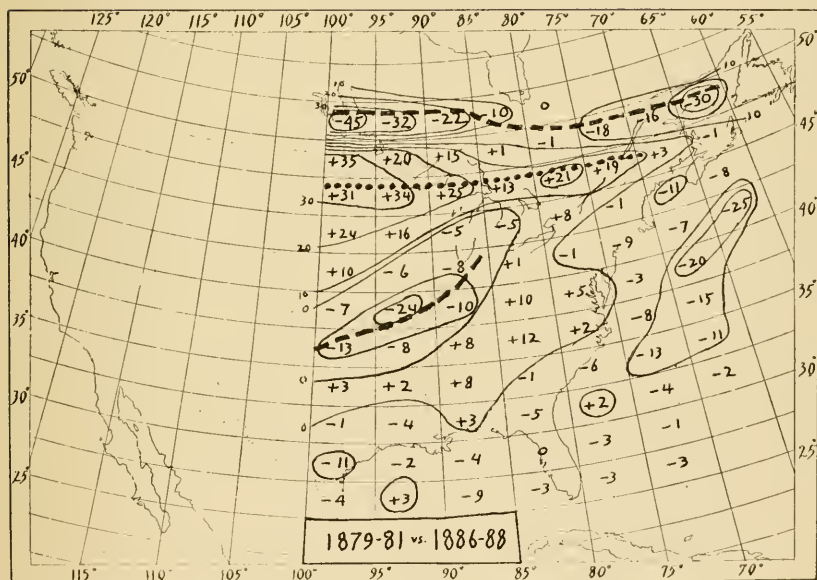


FIG. 15.



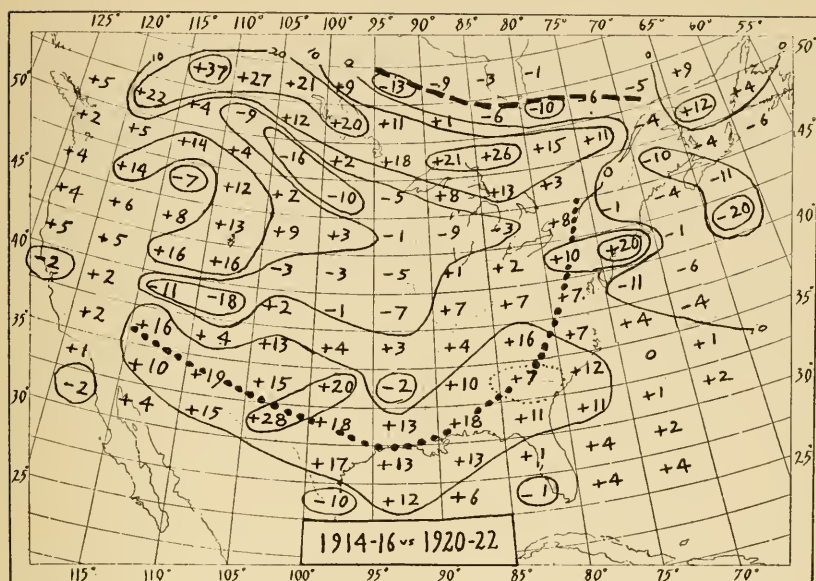


FIG. 18.

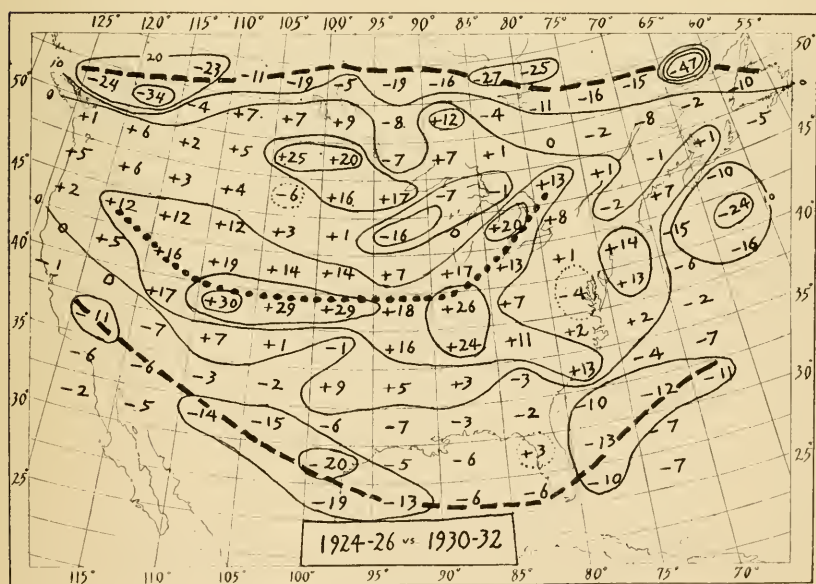
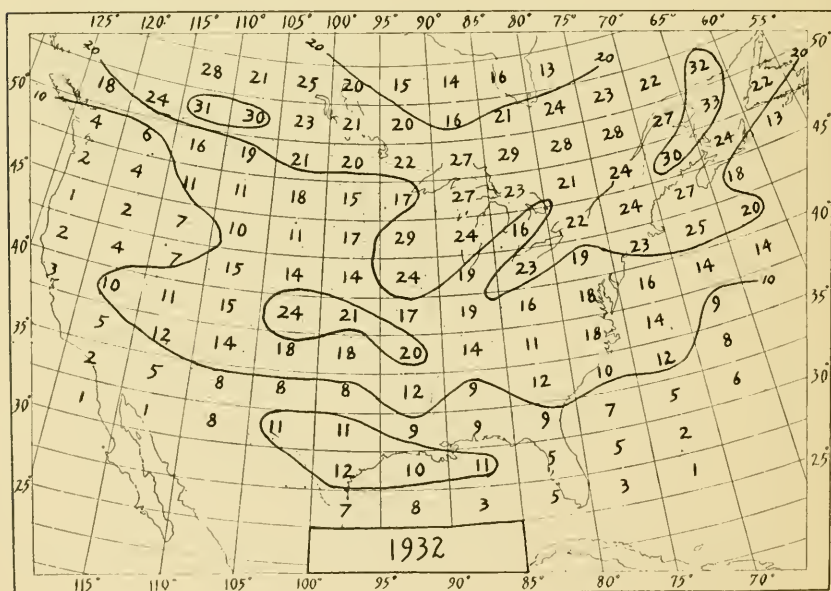
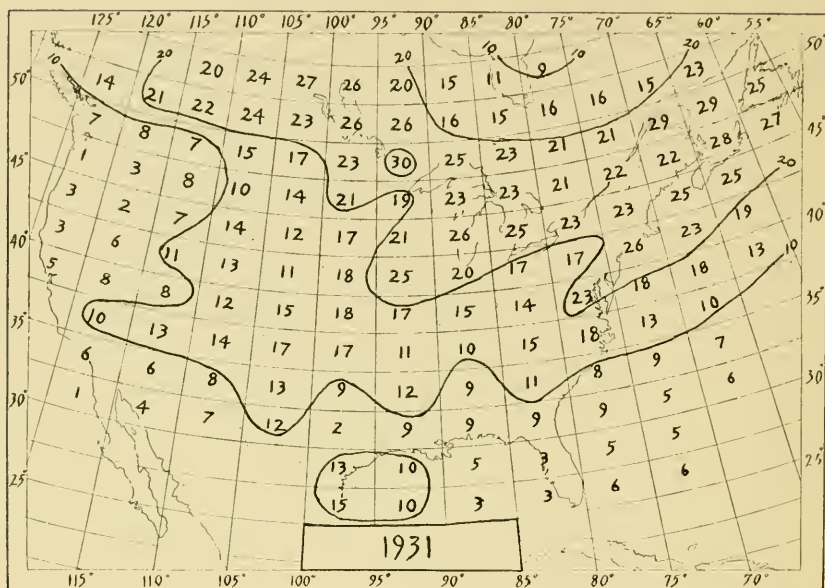


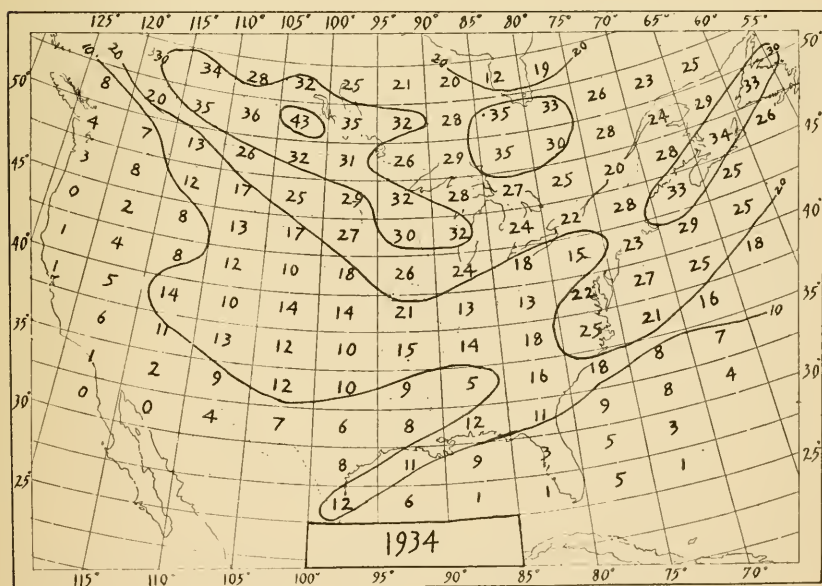
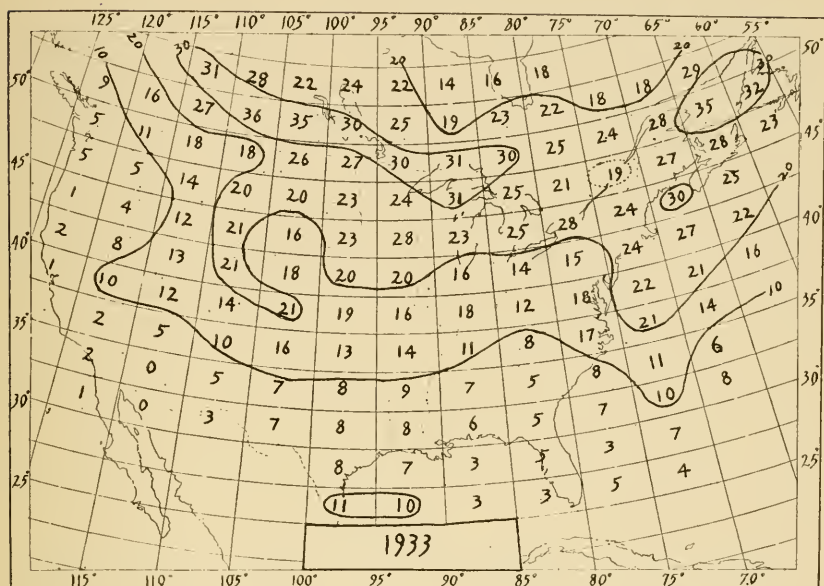
FIG. 19.



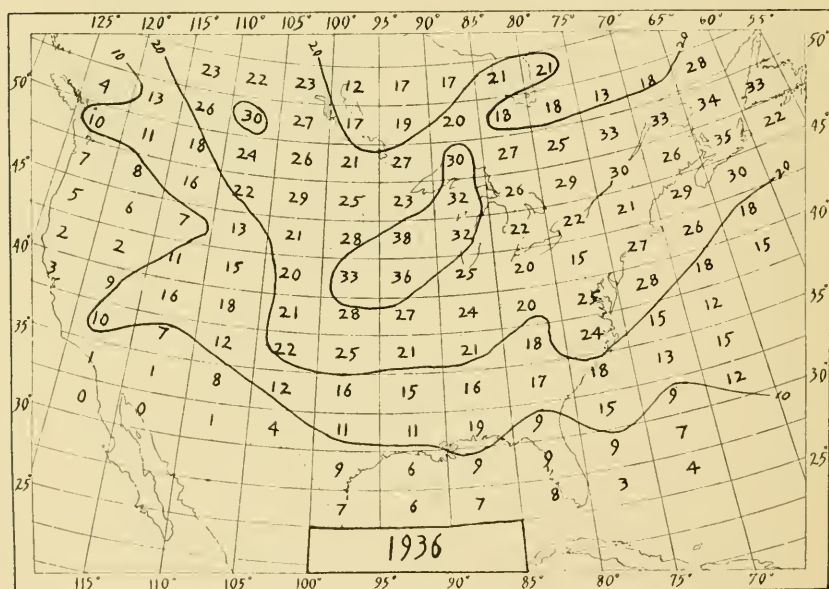
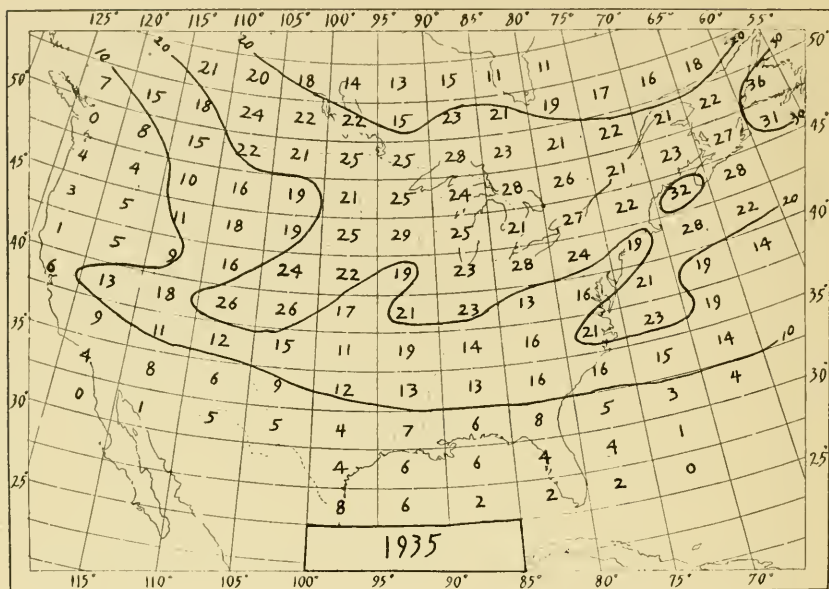
1931 and 1932



1933 and 1934



1935 and 1936































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